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Savanna canopy trees under fire: long-term persistence and transient dynamics from a stage-based matrix population model

PATRICIA A. WERNER[1,†] AND STEPHANIE J. PEACOCK[2,3]

[1]*Fenner School of Environment and Society, Australian National University, Bldg 141 Linnaeus Way, Canberra, Australian Capital Territory 0200 Australia*

[2]*Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2 Canada*

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Abstract. Fire is a major disturbance driving the dynamics of the world's savannas. Almost all fires are set by humans who are increasingly altering fire timing and frequency on every continent. The world's largest protected areas of savannas are found in monsoonal northern Australia. These include relatively intact, tall, open forests where traditional indigenous fire regimes have been largely replaced in the past half century by contemporary patterns with trees experiencing fire as often as three out of five years. Eucalypt canopy trees form the basic structure of these savannas and changes to the canopy due to fire regimes cascade to affect other plants and animals. In this study, we used data from nearly three decades of field studies on the effects of fire on individual trees to define eight life-history stages and to calculate transition rates among stages. We developed a stage-based matrix population model that explicitly considers how fire season and understory influence growth, survival, and recruitment for each life-history stage. Long-term population growth rates and transient population dynamics were calculated under five different fire regimes, each in two understory types, using both deterministic and stochastic simulations of seasonal timing of fires. We found that fire was necessary for long-term persistence of eucalypt canopy tree populations but, under annual fires, most populations did not survive. Population persistence was highly dependent on fire regime (fire season and frequency) and understory type. A stochastic model tended to yield higher population growth rates than the deterministic model with regular, periodic fires, even under the same long-term frequency of fires. Transient population dynamics over 100 yr also depended on fire regime and understory, with implications for savanna physiognomy and management. Model predictions were tested in an independent data set from a 21-yr longitudinal field study in Kakadu National Park. This study is a novel and integrative contribution to our understanding of fire in savanna biomes regarding the potential for long-term persistence and transient dynamics of savanna canopy tree populations. The model is relatively simple, generalizable, and adaptable for further investigations of the population dynamics of savanna trees under fire.

Key words: eucalyptus savanna; fire frequency; fire season; Kakadu National Park; matrix population model; population viability; savanna physiognomy; sensitivity analysis; sorghum; stochastic disturbance; transient population dynamics; variable environments.

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[3] Present address: Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary, Alberta T2N 1N4 Canada.

† **E-mail:** wernerpa@ufl.edu

Introduction

Savannas are tropical and subtropical sparsely wooded grasslands covering ~17% of the earth's land area. Savannas are the most frequently burnt biome in the world (Chuvieco et al. 2008). Collectively, their fires release an estimated 44% of global carbon emissions from biomass burning on the earth (van der Werf et al. 2010). Almost all fires are deliberately lit by humans, both traditionally and contemporarily. The frequency and timing of human-set fires are being increasingly altered, and the rate of conversion of land-use exceeds that of tropical forests (Grace et al. 2006).

The largest protected area of savanna in the world is in north-central Australia (the Top End) and includes Kakadu National Park (KNP), a World Heritage-listed site. Annual precipitation averages >1200 mm/yr among sites across the region and the biome is classified as humid or mesic savanna. The region is characterized by a monsoonal climate with distinct and strong annual precipitation cycles, highly flammable understory, very high incidence of fires, few or no large grazing mammals, largely intact flora and fauna, relatively few introduced species, no history of plowing or a forest industry, and a largely rural, sparse human population (<0.1 per km^2; Stoeckl and Stanley 2007).

Indigenous peoples have occupied these savannas for >50,000 yr and have used fires extensively. When sparse European colonization began <160 yr ago, traditional fire regimes were modified, most significantly over the past ~50 yr. Although human population density remains very low, a high portion of land is burnt per year. For example, an average of 36% of the area of western Arnhem Land was burnt each year from 1990 to 2008 (Oliveira et al. 2013) and 46% of the area of Kakadu National Park was burnt each year from 1980 to 1994 (Russell-Smith et al. 1997). The percentage of land burnt in Kakadu was as high as 70% in 2014 and 2015 (cf. Fire map in Appendix S1) but was reduced to 30% in 2016 and 2017 with a change in management (Parks Australia 2016). Progress has been made in recent years to understand fire regimes and their effects on savanna biota (cf. Russell-Smith et al. 2009, 2013).

More than 70% terrestrial landscape the Australian humid savanna is occupied by forests and woodlands (Parks Australia 2016). The most obvious and widespread of these wooded savannas, covering more than half of the area, are stands of tall (15–25 m height) eucalyptus trees, forming semi-closed canopies, known locally as open forest (cf. Haynes et al. 1991, Wilson et al. 1996, Andersen et al. 2003*a*, Parks Australia 2016; cf. photos in Appendix S1). The largest trees are estimated to be 150 to more than 300 yr old (Werner 1986, Cook et al. 2005). The open forest canopy trees form the basic structure of the savannas and provide resources for native birds, mammals, and reptiles (Woinarski et al. 2001, Woinarski 2011, Lawes et al. 2015).

Are the tall, eucalyptus canopies in these savannas sustainable in the long term, given contemporary fire regimes? To understand the answer to this question, we have developed a stage-based matrix population model of the major canopy trees under various fire regimes, providing a useful tool to project future population numbers, size distributions, and savanna physiognomy, both in the long-term and over transitional periods.

Matrix population models have proven an effective way to integrate life histories and environment in many other ecological systems (Silvertown and Charlesworth 2001, Caswell 2001, 2014, Caswell et al. 2018). For plants, such models can be particularly powerful tools for assessing population viability or recovery in highly variable environments (cf. Tuljapurkar 1990, Caswell 2000, Caswell and Kaye 2001, Tuljapurkar et al. 2003, 2009, Koons et al. 2005, Boyce 2006, Buckley et al. 2010, Ellis and Crone 2013, Davison et al. 2013, Compagnoni et al. 2016, McDonald et al. 2016, Needham et al. 2018 and references therein).

Stage-based matrix models have been applied to canopy trees in two other savanna biomes: the Brazilian cerrado (Hoffmann 1999, Hoffmann and Moreira 2002 for two canopy species as well as two shrubs and a subshrub) and the pine savanna of Georgia, USA (Platt et al. 1988, for the single dominant canopy tree species). Stage-based matrix models of savanna plants other than dominant canopy trees include those for an annual grass species in Australian savanna (Watkinson et al. 1989), a perennial grass species in Venezuelan llanos (Silva et al. 1991), an

endemic tall conifer found only on bluffs and ravines in eastern Florida and Georgia (Schwartz et al. 2000), and two fire-sensitive tree species found mainly in rainforest but occasionally in small groves in Australia savannas (Price and Bowman 1994, Bowman et al. 2001, Trauernicht et al. 2016).

Obtaining the requisite information on tree life histories in harsh environments to build population models is challenging for several reasons. Recruitment of new individuals into the population is relatively rare, often little is known about the fate of the commonly persistent small trees of unknown age, the established canopy trees are long-lived, and so directional change in populations can be slow and subtle. As a result, the population consequences of variation in life histories cannot be fully explored because all three demographic parameters (i.e., survival, growth, and reproduction) are often unknown (Franco and Silvertown 2004). Further, a hierarchy of external and intrinsic factors, often operating on different timescales, can affect savanna tree dynamics, from landscape-scale variables (e.g., fire) to local environments around individual trees (e.g., competition) and from biological attributes (e.g., phenology, height) to types of responses (e.g., growth, death; cf. Figure 1 in Werner and Prior 2013).

Here, we calculated model parameters using data from several field studies conducted over a period of more than 25 yr. These data include annual monitoring of permanently marked individual saplings and mature trees over two decades and the responses to experimentally set fires by permanently marked sub-adult trees (a life-history stage usually excluded in demographic studies of woody savannas; Midgley et al. 2010). Our goal was to determine the fire season and understory type that result in positive population growth (and hence, long-term persistence) of the eucalypt woody canopy. We explored different combinations of fire season, frequency, and interannual timing (i.e., deterministic and stochastic) in two understory types, considering both the long-term population growth rate and the short-term dynamics (i.e., transient behavior). As a test of the model, we compared predicted numbers of trees to the actual number in four field sites after 21 yr of known fire history.

This study highlights the critical life-history stages and fire-understory dynamics that underlie the long-term persistence of the woody canopy trees in the highly variable Australian savanna. The results can inform management about the effects of various fire regimes on the viability and size/stage distributions of canopy tree populations and contribute to a general understanding of how woody trees are maintained in the world's humid and mesic savannas.

Study System

Site overview

Tropical savannas in Australia cover an area of >1.9 million km^2, ~25% of the continent. They occur in a wide band across the north, extending 3400 km from the Atherton Tableland in eastern Queensland westward to just beyond the Kimberly region in Western Australia. Eight biogeographic regions are commonly recognized (Stoeckl and Stanley 2007). Our study focuses on the >200,000 km^2 north-central region containing humid and mesic savannas. The region contains the capital region of Darwin and eastward to include the sparsely populated Alligator Rivers Region (ARR) and the vast Arnhem Land. Both the ARR and Arnhem Land were largely free from non-indigenous activities until ~75 yr ago (Haynes et al. 1991).

The data used to parameterize our models were derived from experimental field studies conducted in Kapalga Research Station (12°34′ S, 132°22′ E), a limited-access site of 670 km^2 located within the northern sector of KNP. Kakadu National Park is the largest protected area of savanna in the world, encompassing 19,804 km^2 and an entire river basin within the Alligator Rivers Region (ARR). It was named a World Heritage site by UNESCO in 1981. Kakadu National Park remains sparsely populated with <2000 residents but caters to ~200,000 visitors per year (Parks Australia 2016). The broader region is also sparsely populated with the vast aboriginal-owned Arnhem Land as an eastern border of the Park, the 3000 km^2 Nitmiluk National Park to the south, and military lands and protected wetlands to the west. Kakadu National Park is managed jointly by local aboriginal peoples (Bininj/Mungguy) and the Commonwealth government (Parks Australia 2016).

Fifty-five percent of KNP is classified as open forest (typically trees 15–25 m height and ~60% projected ground cover), and representative of the humid and mesic savannas of the larger region. The broader terms wooded savanna or lowland wooded savanna are applied to all wooded areas (including open forest, monsoon rainforest, stands of shorter tree species on shallow soils, and woody scrub) found in the lowlands in contrast to vegetation on the high eastern escarpment or stone country. In total, lowland wooded savanna covers 70% of KNP (Parks Australia 2016).

Descriptions of the geology, climate, and vegetation the larger region, KNP and Kapalga are detailed in Haynes et al. (1991), Press et al. (1995), Finlayson and von Oertzen (1996), Wilson et al. (1996), and Andersen et al. (2003*a*).

Fire is used as a major management tool in KNP, both traditionally and today (Russell-Smith et al. 2003*a*, 2009, 2013, Parks Australia 2016). Of the total area of lowland savanna open forests and woodlands, ~55% has burned every year since the mid-1980s when modern techniques for landscape-scale record keeping began (Gill et al. 2000, Russell-Smith et al. 1997, 2003*a*, 2009, Russell-Smith and Edwards 2006, Andersen et al. 2005; cf. *Study system*: *Fires* and *Discussion*: *Implications for savanna physiognomy*.)

Seasonality

Precipitation is the main marker of seasonality across the north-central humid savannas, with ~84% of total annual precipitation occurring over a distinct single wet season from approximately December to May with the remaining 16% from April to November (Andersen et al. 2003*a*; Fig. 1a). In 35 yr of rainfall records, no rain fell during June for 27 yr and no rain fell during July or August for 29 yr (Jabiru Airport in northern KNP, Bureau of Meteorology), highlighting the extreme dry season. Data on mature trees used in the current study came from periods when wet season precipitation ranged from 1049 to 1685 mm/yr and dry season rainfall ranged between 0 and 61 mm/yr (Werner 2005, 2012).

The interannual variation in total rainfall in these subcoastal humid Australian savannas is considered very low (Australian Bureau of Meteorology, from 96 yr of annual rainfall data) in spite of the strong seasonal pattern within years.

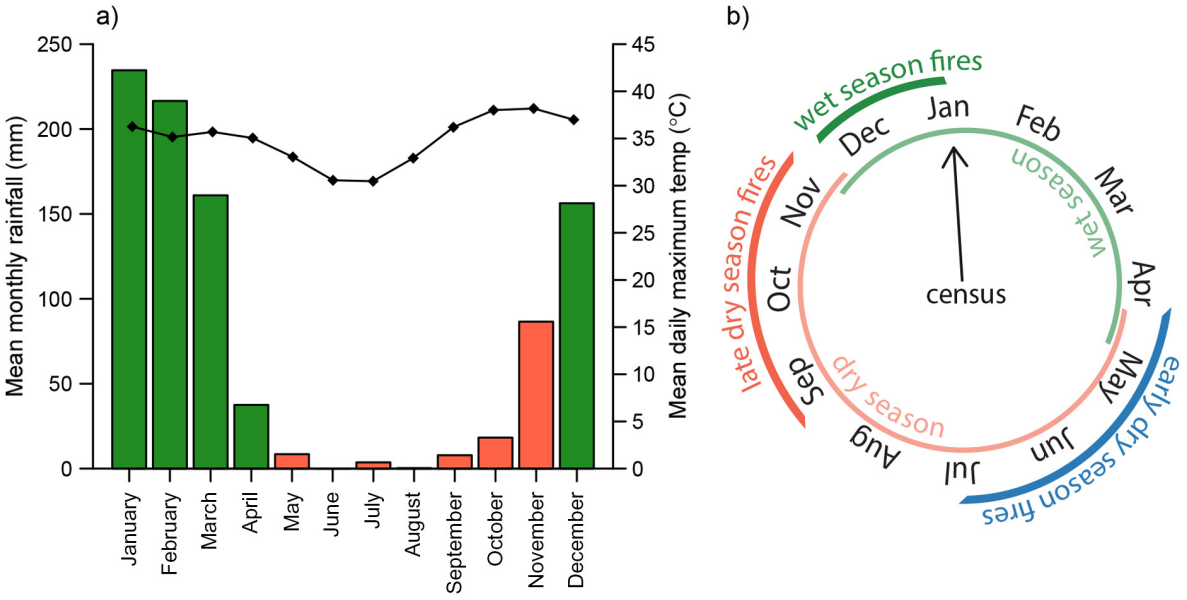

Fig. 1. (a) Mean monthly rainfall (mm) and mean daily maximum temperature in Darwin, Northern Territory, Australia (Australian Bureau of Meteorology). (b) Yearly cycle of precipitation showing dry season (inner circle), and the three periods of fires used in our models (outer circle). Timing varies year to year and is approximate.

This contrasts with moderate to high interannual variability in rainfall as one moves eastward and southward into semi-arid savannas of the continent and where precipitation variability plays a larger role in tree population dynamics (Williams et al. 1996, Liedloff and Cook 2007, Fensham et al. 2017).

The annual shift from wet season to dry season occurs rather abruptly with a shift in the prevailing monsoonal winds of the region. Then as the dry season progresses, fire weather becomes more severe, characterized by drier vegetation, lower humidity, stronger winds, and often higher temperatures, with the result that fires later in the dry season tend to be more intense than those earlier in the dry season (Gill et al. 1996, Williams et al. 1998, Russell-Smith and Edwards 2006).

Fires

Humans are the ignition source for almost all dry season fires of the region. For tens of thousands of years, indigenous peoples lit fires for several purposes such as hunting, clearing areas around camps or walking areas, and creating mosaics of burnt vegetation that reduced the extent of possible late dry season fires or lightning-set fires in the early wet season (cf. Haynes 1985, Yibarbuk et al. 2001, Russell-Smith et al. 2009, 2013). Today, most fire ignitions in the region are made by land managers including Aboriginal residents, protected area managers, pastoralists, and military personnel, as well as by casual visitors and unauthorized persons (Russell-Smith et al. 2003*a*, 2013).

Fires caused by lightning are relatively rare (e.g., 4% of the area in KNP over a 15-yr period reported by Russell-Smith et al. 1997). Lightning-ignited fires generally occur during dry storms in the first two months of the wet season. Lightning-ignited fires that occur early in this period can have similar effects on vegetation to late dry season fires and can burn over a large area if the area has not been burnt for some time (Murphy and Russell-Smith 2010).

Three major types of fires are commonly identified in many analyses of contemporary fires in this region: early dry season fires in May to early July, late dry season fires in September to November, and early wet season fires in December to January (Gill et al. 1996, 2000, Williams et al. 1998, 2003*a*, Andersen et al. 2003*a*, Russell-Smith et al. 2003*a*, 2007, 2013, Russell-Smith and Edwards 2006). The fire types are differentiated by recent weather rather than calendar months per se because the start and duration of the dry season naturally vary from year to year (Taylor and Tulloch 1985).

Early dry season fires are almost always slow-moving, trunk-scorching, ground fires of low intensity, usually creating incomplete, patchy burn patterns (Gill et al. 1996, 2000, 2003, Williams et al. 1998, 1999*a*, 2003*a*, Russell-Smith and Edwards 2006, Murphy and Russell-Smith 2010, Werner 2010; cf. photos in Appendix S1). Rarely, early dry season fires may be of high intensity and/or with little patchiness when fires are not allowed to burn naturally (e.g., if unburnt patches left after a fire are relit or if ringing fires around a defined area are used, as in some experimental treatments; Bowman et al. 1988, Andersen et al. 2003*a*) or if the site has not burnt for a long time (Williams et al. 2003*a*, Russell-Smith and Edwards 2006, Murphy and Russell-Smith 2010). Early dry season fires, with their inherently patchy, unburnt portions, were a major feature of traditional Indigenous management practices and attempts to reproduce this aspect of fire management are championed today (Russell-Smith et al. 2009, 2013).

Late dry season fires are generally rapidly moving, canopy-scorching fires, of moderate to high intensity, usually with little patchiness at ground level because of drier fuels and fire weather conditions (Gill et al. 1996, 2000, 2003, Williams et al. 1998, 1999*a*, 2003*a*, Russell-Smith and Edwards 2006; cf. photos in Appendix S1). In an analysis of fires in two national parks of the region, >50% of late dry season fires were classified as moderate to severe (Russell-Smith and Edwards 2006). Where a late dry season fire followed a previous fire, 23% were classified as severe, but when time since the previous fire was 5 yr, 43% of late dry season fires were classified as severe (Murphy and Russell-Smith 2010).

Wet season fires occur most often in the early wet season when precipitation is intermittent, allowing for vegetation that is dry enough to carry fire. The earliest of these fires can have characteristics similar to late dry season fires, whereas later wet season fires may be of low intensity but slow-moving with relatively long

residence times, depending on fuel, moisture, and weather (Russell-Smith and Edwards 2006). Early wet season fires mainly occur naturally due to lightning; they were not traditionally set by indigenous peoples and today are rarely lit by land managers, but occasionally may be lit by others as an act of vandalism.

As in most savannas, fires are mainly ground (not canopy) fires, although some may include the mid-story or even attain intensities which scorch or burn the lower leaves of the tallest trees, depending on such factors as season, fuel biomass, wind speed, and time of day. Other factors (e.g., type of fuel, humidity, ignition method, and time since previous fire) may influence fire intensity and/or severity of effects on vegetation (Gill et al. 1996, Williams et al. 1999*a*, 2003*a*, Murphy and Russell-Smith 2010). Midgley et al. (2010) have concluded that the relationship between fire intensity and fire season in savannas is far from being understood.

Fuel loads (biomass) generally reach maximum levels within 2–5 yr of no fires (e.g., in Kapalga; Cook 2003) in these open forests. Fuel loads remain high only in unburnt experimental sites (e.g., Kapalga; Andersen et al. 2003*a*, Cook 2003), in unburnt preserves (e.g., Solar Village; Woinarski et al. 2004; and Territory Wildlife Park; Scott et al. 2012), on sites topographically protected from fires (e.g., monsoon rainforest; Bowman 1992), and on sites near settlements where fire is suppressed (Russell-Smith and Edwards 2006, Murphy et al. 2014).

For our model, we used field data from study sites in Kapalga where the most common fire intensity occurred for each fire season. Fires were allowed to burn naturally (e.g., unburnt patches were not relit). Fuel loads were 3.7 t/ha ± 1.2 (mean ± standard deviation; P. A. Werner, *unpublished data*) in 1982 at the beginning of the field studies, which is well below that reported for long-unburnt sites in Kapalga (8.3 t/ha ± 2.7; Cook 2003). The subsequent early dry season fires were of low intensity, and the late dry season fires were of high intensity (Werner 2005, 2012).

Understory

We categorized the understory into two types—sorghum and non-sorghum—that produce very different burn patterns of early dry season fires, represent different competitive environments for sub-adult trees, and have different effects on saplings when a fire occurs (Werner 2010, 2012, Werner and Franklin 2010, Werner and Prior 2013). Smaller life-history stages are especially affected by understory vegetation. For example, understory vegetation suppressed juvenile tree growth in experimental field studies humid savannas of northern Australia (where the effect was ameliorated by grazing; Werner et al. 2006).

Sorghum.—Sorghum understory is dominated by speargrass, a native annual C_4 grass, *Sorghum brachypodum* Lazarides (formerly *Sorghum intrans* F. Muell. and *Sarga intrans* (F. Muell) Spangler), hereafter termed sorghum. Sorghum is widespread and provides the main natural fuel for fires in the region. Mature plants are mainly single stems, forming tall stands (often >1.5–3.0 m in height; cf. photos in Appendix S1) of up to 200–400 stems per m^2 (Andrew and Mott 1983, Watkinson et al. 1989) and often with >80% ground cover (Werner 2010). This annual plant has no dormant seed bank; seeds germinate at the start of the following wet season and resulting plants mature, set, and disperse new seed. The plants then die back before the end of that wet season, before seasonal senescence by most other grasses and herbaceous forbs (cf. photos in Appendix S1), crumpling into a perched, aerated, and easily ignited fuel by the time the early dry season fires begin (Andrew and Mott 1983, Andrew 1986). Although ground-level fuel loads on sites with sorghum understory tend to be less than those with non-sorghum, sorghum grass is particularly flammable and produces more intense and less-patchy fires than does non-sorghum herbaceous vegetation (Elliott 2005).

Sorghum understory is usually quite persistent and resilient when established on a site in these fire-prone environments because most of its life history plays out during the favorable wet season. However, if left unburnt, sorghum populations decline within a few years (Andrew 1986) because the young plants of these annuals do not thrive when shaded, whether by litter or other herbaceous species. Fires remove sources of understory competition and shade and thus promote a sorghum understory. Nonetheless, because sorghum does not have a seed bank, a stand can be removed suddenly and entirely by a

wet season fire that occurs after the seedlings have appeared with the first rains and are >1 cm in height (Press 1987, Cook et al. 1998, Miles 2003).

Non-sorghum.—The second main type of understory vegetation is made up mainly of a mixture of native herbaceous forbs with rosettes and/or one to a few branching stems, and small annual and perennial native grasses 20–150 cm in height (Williams et al. 2003*b*, Werner et al. 2006, Werner 2010; cf. photos in Appendix S1). This understory may also include shrubs and non-eucalypt woody species that tend to be deciduous in the dry season and are generally very fire sensitive (Scott et al. 2012). The non-sorghum understory is often persistent in areas long unburnt as well as within otherwise dense patches of sorghum (often several meters in diameter; Andrew 1986). The perennials in the non-sorghum plots tend to remain green well into the dry season (cf. photos in Appendix S1) creating sustained competitive pressure on juvenile and sapling trees for the dwindling underground resources, in contrast to the early drying of the annual grass in the sorghum plots (Werner 2010, 2012).

For the current study, we have used data from both sorghum understory with 40–80% (mean = 70%) ground cover of sorghum and non-sorghum understory with 0–20% (mean = 7%) ground cover of sorghum, as described in Werner (2010, 2012) and Werner and Prior (2013).

Canopy trees

Population.—Two native species, *Eucalyptus tetrodonta* F. Muell. and *E. miniata* A. Cunn. ex Schauer (family Myrtaceae), dominate the canopy stratum of the vast humid savannas of northern Australia. In KNP, sub-dominants in the canopy include a scattering of other myrtaceous species such the bloodwoods, most often *Corymbia porrecta* (ST Blake) KD Hill and LAS Johnson, and in much lesser abundance *C. bleeseri* (Blakely) KD Hill and LAS Johnson, or *Xanthostemon paradoxus* F. Muell., all formerly classified as *Eucalyptus*.

At our study sites in Kapalga, these myrtaceous species collectively make up 87% of all adult trees in the open forests on the ridges and slopes (Werner 2005). Of sub-adult trees, 94% of individuals are of just three species: *Eucalyptus tetrodonta*, *E. miniata*, and *C. porrecta* (termed eucalypts; Werner and Prior 2013). These three species collectively make up the bulk of the canopy layer are considered together as the population that is the focus of this study.

Although it is unusual to use multiple species collectively to comprise a population, it is not unheard of (e.g., desert annuals in Goldberg et al. 2001 and examples of studies comparing plant life histories, demographics, strategies, lifeforms, and coexistence in Silvertown and Charlesworth 2001, Henriques and Hay 2002, Grime 2006). In our study, it is justified because the rates of growth, survival, and reproduction, and responses to fire are very similar among the three species (Appendix S2). In various studies, the range of rates observed within a species is greater than the differences in average rates among species. Further, statistical analyses have revealed several significant explanatory factors for responses to fire when the species are considered collectively but are not important for individual species (Appendix S2).

In Appendix S2, we have provided detailed summaries of the results of various studies on the growth, survival, reproduction, phenology, and ontogenetic changes of the canopy tree species. These biological and ecological patterns underpin the development of both the life-history stages of our model and the vital rates from one stage to another.

Stages.—We structured the population by stage, rather than age because the ages of the eucalypt trees are rarely known. Trees can persist as juveniles for many years, recovering from underground stores after being burnt to the ground, often several times (Williams et al. 2003*b*, Lawes et al. 2011, Clarke et al. 2012, Werner and Prior 2013, Freeman et al. 2017). Further, most mature trees have hollow boles (Werner and Prior 2007) and thus no early annual growth rings.

We divided the population into $m = 8$ different stages: seedlings, small juveniles, large juveniles, small saplings, large saplings, poles, adults, and large adults (Table 1). These stages are based on morphological and phenological characteristics and on ecologically relevant differences in growth and survival under various environmental conditions, including fire season

and understory type (Werner 2012, Werner and Prior 2013; Appendix S2).

For larger trees, diameter at breast height (dbh) is the major factor determining growth and survival over the following year (Werner 2005) and was used to distinguish poles, adults, and large adults (Table 1). For sub-adult trees, maximum height is an important explanatory factor for responses to competition and fire (Werner and Franklin 2010, Werner 2012, Werner and Prior 2013) and was used to delineate stages for sub-adult trees (Table 1). The delineation of these stages was based on biological features that maximize homogeneity within a stage based on previously reported variability in growth and survival and considered class width and number of stages, as either can affect calculations of population growth rates and/or sensitivities or elasticities (cf. Vandermeer 1978, Enright et al. 1995, De Kroon et al. 2000, Easterling et al. 2000, Caswell 2001, Niklas et al. 2003).

We did not include a seed stage because seeds and germination occur within a single year (Appendix S2); hence, the reproduction rate is between mature tree to seedling stage in any given year. The appearance of new juveniles from underground (non-seed) sources is rare, mainly confined to areas where the canopy has been removed altogether (Appendix S2). Because the environmental causes, growth, and demographic fate of such juveniles are unknown, we did not include them as a separate stage in our basic model.

Table 1. The eight life-history stages in the stage-structured matrix model, classified by height and diameter at breast height (dbh).

Stage number	Stage name	Criterion
1	Seedling	<1 yr old at time of census (January)
2	Small juvenile	<0.5 m height
3	Large juvenile	0.5 to <1.50 m height
4	Small sapling	1.50 to <3.00 m height
5	Large sapling	3.00 to <5.00 m height
6	Pole	5.00 to <10.0 cm dbh
7	Adult	10.00–34.99 cm dbh
8	Large adult	≥35.00 cm dbh

Notes: dbh takes precedence over height of plant; that is, once a tree attains a dbh of 5.00 cm, it becomes a pole, adult, or large adult category.

Model

We developed a stage-based population model that integrated various studies of survival, growth, and reproduction under different fire regimes in two main understory types. Our goal was to explore conditions that might result in long-term viability of savanna canopy trees. Here, we present the general form of matrix population models as well as the specific form of our model including the life-history stages and the parameterization of transition matrices. For a thorough introduction to the mathematical properties of matrix models, see Caswell (2001, 2014) and Caswell et al. (2018).

General model form

The general form of a stage-based matrix population model is

$$\vec{N}_{t+1} = \boldsymbol{A}^t \vec{N}_t, \quad (1)$$

where $\vec{N}_t$ is a vector of length m describing the number of individuals in each of m stages at time t and $\boldsymbol{A}$ is an $m \times m$ transition matrix. The transition matrix has elements a_{ij}, where the first row ($i = 1$) describes the number of offspring produced by individuals in stage j that survive to $t + 1$ (which we refer to as recruitment) and all other a_{ij}'s with $i > 1$ to describe the probability of an individual surviving and transitioning from stage j to stage i. This definition of transition probability includes the probability of surviving and remaining in the same stage, which is simply a_{ij} where $i = j$. Mortality does not appear as a term in the matrix but can be calculated as the probability of not transitioning (i.e., $M_j = 1 - \sum_{i=2}^{m} a_{ij}$).

For any time-step t, the solution to the model equation (1) can be calculated given an initial number of individuals in each stage, $\vec{N}_0$

$$\vec{N}_t = \boldsymbol{A}^t \vec{N}_0. \quad (2)$$

The transition matrix $\boldsymbol{A}$ provides information on the long-term trajectory of a population, even in the absence of population abundance data. If the matrix meets certain properties (i.e., is irreducible and primitive; Perron 1907, Frobenius 1912), there exists a simple, positive, real eigenvalue of the transition matrix that is larger than

all others. Biologically, this dominant eigenvalue represents the long-term growth rate of the population and is commonly denoted by λ. All the transition matrices in this study possessed such an eigenvalue.

The corresponding eigenvector of the dominant eigenvalue gives the stable stage structure of the population (i.e., the distribution of individuals among the stages). Once the population reaches that stable stage structure, the number of individuals in each stage will grow by a factor of λ each year. If $\lambda > 1$, the population will grow and if $\lambda < 1$, the population will eventually be extirpated. The sensitivity of the population growth rate, λ, to changes in the parameters of the transition matrix is of key interest. These sensitivities are calculated as the rate of change in λ in response to small changes in the matrix elements and are computed numerically or more often analytically as $\partial\lambda/\partial a_{ij}$.

In applying the matrix modeling approach, we assumed that the population was closed (i.e., no immigration or emigration). We also assumed that recruitment, survival, and stage transitions were density independent (there was no evidence for density dependence in the studies we used to parameterize our model). Further, we assumed that within a given stage, the rates of growth and survival were constant for each environmental condition. Justification for and potential consequences of the two final assumptions are discussed in Appendix S3.

For our analysis of the matrix model, we used the open-source statistical software R (R Core Team 2016), specifically the popBio package (Stubben and Milligan 2007) for calculating growth rates and sensitivities. The R code to reproduce all simulations is available online at https://github.com/sjpeacock/WernerPeacock2017.

Parameterization of transition matrices

Transition matrices were developed for eight different environments representing a combination of four different seasons of fire (hereafter termed fire type) that occurred that year (N, no fire; E, early dry season fire; L, late dry season fire; W, wet season fire) and two different understory types (1 or S, sorghum; 2 or NS, non-sorghum). No single field study covered the entire lifecycle of eucalypts. Therefore, the recruitment and transition probabilities (vital rates) were parameterized based on multiple studies. Data on established trees were from several experimental field studies by P. A. Werner and colleagues conducted in Kapalga, KNP, between 1982 and 1990 in sites near, but outside of, the fire compartments used in the five-year (1990–1994) CSIRO fire experiment (Andersen et al. 2003*a*). Data we used for recruitment, seedling survival, juvenile and sapling transitions, and pole and adult transitions came from several sources.

The assignment of trees to a stage depends on the census time when individuals are counted and measured. Our census time was January, at the start of the wet season and well after germination of seeds that had been produced during the previous year (Fig. 1b). Thus, the transition matrix describes the stage transitions from January through December, with a time-step of one year.

Recruitment.—Flowering and seed production occur in the dry season (Setterfield and Williams 1996, Williams et al. 2003*b*), with peak seed fall up to one month before or during early wet season rains (Russell-Smith and Setterfield 2006). Rates of granivory are very high, both pre-dispersal and post-dispersal (Setterfield and Williams 1996, Andersen and Lonsdale 1990). Germination of any remaining seed occurs early in the wet season (Setterfield and Williams 1996, Williams et al. 1999*b*, 2003*b*).

We did not include a seed stage in our models but considered recruitment into the population at the seedling stage (the addition of new individuals to the population). This was possible because the model census period occurred in January (early wet season) and thus generally spanned the reproductive period from the production and dispersal of seed by mature trees to seed germination and seedling establishment. This census time also avoided an unnecessary complication of accounting for high interannual variability in seed production (Setterfield and Williams 1996, Williams et al. 1999*b*, 2003*b*). Thus, the recruitment parameters a_{ij} were the number of seedlings produced by an individual of stage j during the one-year time-step of the model; these were the result of seeds that were produced, germinated, and survived as seedlings at census time in January.

Poles, adults, and large adults are capable of flowering and producing viable seeds and

seedlings. We calculated base values for recruitment for each of these stages based on data of the known appearances of new plants in unburnt plots of known size and known numbers of trees large enough to have produced seeds/seedlings (P. A. Werner, *unpublished data* from the field study reported in Werner et al. 2006). These values were within the range of our estimates of seedlings per individual tree derived from independent data on numbers of seedlings per unit area in unburnt plots reported in Williams et al. 2003*b* (data from Setterfield 1997, 2002). In a year with no fire, we considered that a pole successfully produced one seedling, and an adult and a large adult each produced two seedlings.

Fires have a devastating effect on recruitment into the population as demonstrated by both observational and experimental studies (Setterfield 1997, 2002, Williams et al. 2003*b*). We assumed that recruitment (seedling establishment) was reduced if there was a fire relative to the patchiness of the burn (i.e., the probability that a given tree would be burned if a site had burned, Pr(burn)). For example, during late dry season fires, 100% of the ground tends to be burnt and recruitment therefore would be zero, but for early dry season and wet season fires, a percentage of the landscape remains unburnt (1-Pr(burn)) so the potential for seedling survival is not zero. For these fires, the base value for recruitment when fire was absent (above) was multiplied by 1 – Pr(burn) under the given fire type where Pr is the proportion of ground burnt (and hence the probability of being burnt). Data on patchiness of burns were taken from a field study where fires were measured at a microsite scale of 10×10 cm^2 (Werner 2010; Table 2). Potential differences in patch types due to time since previous fire are discussed under future research.

Seedling survival.—Seedlings are defined as new individuals that have appeared within the population within the past year (Table 1), so they cannot survive within the same stage (i.e., $a_{11} = 0$) but must transition to small juvenile stage, assuming they survive to the following census date ($a_{21} > 0$). Setterfield (2002) reported that in the absence of fire, the probability of *E. miniata* seedlings surviving from January to January was ~25% but there was considerable variability due to microsite and weather events.

Table 2. Fire patchiness on a fine scale: the proportion of area that is actually burned under different fire types, assessed on 10×10 cm grid (Werner 2010), in the juvenile plots used in Werner (2012) and Werner and Prior (2013) and used in calculations of recruitment and seedling survival for patchy fires.

	Understory	
Fire type	Sorghum	Non-sorghum
Early dry season	0.947	0.531
Late dry season	1.000	1.000
Wet season	0.986	0.932

Because recruitment and seedling survival are naturally quite low, we chose $a_{21} = 0.5$ as the base value for years with no fire ($f = N$), a value higher than the average seedling survival but within the range reported by Setterfield (2002). For early dry season, late dry season, or wet season fires, the base survival (unburnt) was multiplied by the patchiness of the burn (Table 2) as was done for recruitment (above). For example, in early dry season fires in a non-sorghum understory, a total of only 53% of the microsites were burnt (47% unburnt; Werner 2010); in that case, our calculation would result in a seedling survival value of $a_{21} = 0.50 \times 0.47 = 0.235$.

Juvenile and sapling survival and transitions.—Survival rates and transition probabilities for small juvenile, large juvenile, small sapling, and large sapling stages were taken directly from field data underlying Figure 4 of Werner (2012). In the field, 2405 individual trees were marked and monitored over three years in plots (totaling 7.2 ha) located within larger experimental compartments totaling an area of 20 km^2. The plots had either sorghum or non-sorghum understory but were otherwise matched closely as possible. Each plot was subject to a single fire conducted in the early, late, or wet season, or remained unburnt. All fires were set as set as line-ignition fires (not perimeter or ring fires) and without reignition of any unburnt patches; thus, fires behaved in a realistic, natural landscape pattern. Early dry season fires were judged as low intensity whereas the late dry season and early wet season fires were judged as high-intensity fires,

details in Werner and Franklin (2010) and Werner (2012).

All individual sub-adult trees were assessed repeatedly for survival, stem height, and dbh (Werner and Franklin 2010, Werner 2012, Werner and Prior 2013). Survival of these trees was generally consistent with those from an earlier study where 58 permanently marked sub-adult eucalypts were followed for six years (Werner et al. 2006). Where a resprouting sub-adult tree initially produced multiple stems after the complete loss of above ground biomass, the maximum height of those stems was sufficient to accurately assess recovery and persistence of the individual (Werner and Franklin 2010, P. A. Werner, *unpublished data*), as was the case in a study of six woody species in a pine savanna in North Carolina (Schafer and Just 2014).

Field data indicated that juveniles and saplings can transition up two or even three stages within a year, or revert to a smaller stage if, for example, their height or dbh is reduced due to fire or drought (Williams et al. 2003*b*, Werner 2012, Werner and Prior 2013). These possibilities are reflected in the transition matrices (Fig. 2, Table 3). Downward transitions to smaller stages, although unusual, have been considered in other stage-structured matrix models, for example, for colonies of clonal organisms such as corals that may regress from large adult sizes to small resting stages in seasonal habitats (e.g., Hughes 1984).

Pole and adult transitions.—Transition probabilities for poles, adults, and large adults were calculated from field data reported in Werner (2005). All 487 mature canopy eucalypts in an area totaling 1.8 ha were permanently marked and monitored over nine years, including in unburned plots and after early dry season and late dry season fires (fronting or line fires; described in Werner 2005). Fires were intermittent; that is, they were not repeat fires as in other studies where permanently marked trees were subject to annual or biennial fires over five or 23 yr (Andersen et al. 2003*a* and Russell-Smith et al. 2003*b*, respectively). Unlike the data for juveniles, which were already available as transition probabilities under different fire types and understory, the data for poles and adults consisted of annual mortality and changes in dbh of permanently marked trees and the corresponding fire history. From these field data, we calculated the probability of survival within a stage (i.e., a_{ii}) and the transition probabilities among stages (i.e., a_{ij}, $i \neq j$) as follows.

Poles and adult trees were unlikely to transition more than one stage within a year because the size categories for poles and adults were quite broad. To determine the probability of transitioning up a stage (i.e., a_{ij} where $i > j$), we first

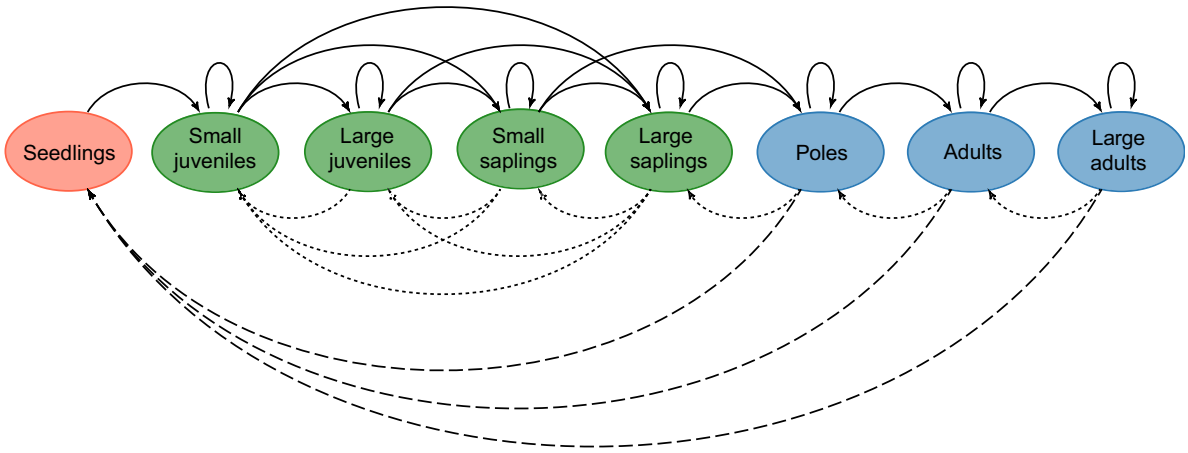

Fig. 2. Model diagram showing the eight stages (cf. Table 1) and the possible transitions among them including survival and growth (solid lines) and survival and reduction to smaller size (dotted lines). Each of these arrows has an associated transition probability (cf. Table 3). Also shown is recruitment of seedlings from poles, adults, and large adults (dashed lines).

Table 3. The transition matrices with base parameters for recruitment and transition probabilities under four fire types and two understory types, assuming patchy fires (Table 2).

Fire season		Sorghum Understory								Non-sorghum Understory							
	to (i)	from (i)								from (j)							
No fire ($f = N$)		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
	1						1.000	2.000	2.000						1.000	2.000	2.000
	2	0.500	0.720	0.140						0.500	0.860	0.280	0.110				
	3		0.190	0.600	0.330						0.100	0.620	0.440				
	4		0.030	0.190	0.370							0.100	0.340				
	5			0.020	0.300	0.840	0.012						0.110	0.340	0.012		
	6					0.160	0.877	0.003						0.160	0.877	0.003	
	7						0.027	0.965	0.004						0.027	0.965	0.004
	8							0.010	0.970							0.010	0.970
	M_j	0.500	0.060	0.050	0.000	0.000	0.084	0.022	0.026	0.500	0.040	0.000	0.000	0.500	0.084	0.022	0.026
Early dry season fire ($f = E$)		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
	1						0.053	0.106	0.106						0.469	0.938	0.938
	2	0.027	0.720	0.590	0.120					0.235	0.780	0.200					
	3		0.210	0.080							0.170	0.660					
	4			0.330	0.350						0.010	0.100	0.440	0.170			
	5				0.470	0.500							0.560	0.160			
	6				0.060	0.500	0.803	0.000						0.670	0.803	0.000	
	7						0.043	0.982	0.002						0.043	0.982	0.002
	8							0.017	0.990							0.017	0.990
	M_j	0.973	0.070	0.000	0.000	0.000	0.154	0.001	0.008	0.765	0.040	0.040	0.000	0.000	0.154	0.001	0.008
Late dry season fire ($f = L$)		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
	1						0.000	0.000	0.000						0.000	0.000	0.000
	2	0.000	0.610	0.080						0.000	0.810	0.050	0.330	0.230			
	3		0.320	0.790	0.330	0.640					0.160	0.710					
	4			0.120	0.670							0.150	0.660				
	5					0.080	0.035					0.020		0.080	0.035		
	6					0.070	0.725	0.011						0.690	0.725	0.011	
	7						0.008	0.969	0.011						0.008	0.969	0.011
	8							0.004	0.864							0.004	0.864
	M_j	1.000	0.070	0.010	0.000	0.210	0.232	0.016	0.125	1.000	0.030	0.070	0.010	0.000	0.232	0.016	0.125
Wet season fire ($f = W$)		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
	1						0.014	0.028	0.028						0.068	0.136	0.136
	2	0.007	0.680	0.360	0.040	0.020				0.034	0.500	0.130	0.060				
	3		0.220	0.430	0.260	0.070					0.400	0.600	0.430				
	4			0.110	0.360	0.120					0.020	0.180	0.260	0.280			
	5				0.330	0.290	0.035				0.020		0.140	0.300	0.035		
	6					0.480	0.747	0.006						0.280	0.747	0.006	
	7						0.026	0.972	0.007						0.026	0.972	0.007
	8							0.010	0.927							0.010	0.927
	M_j	0.993	0.100	0.100	0.010	0.020	0.193	0.012	0.066	0.966	0.060	0.090	0.110	0.140	0.193	0.012	0.066

Notes: The last row (M_j) is not part of the matrices but the probability of mortality, calculated as $M_j = 1 - \sum_{i=2}^{8} a_{ij}$.

selected trees that had a positive annual change in dbh. From these trees, we estimated the average annual increase in dbh for each fire type and stage (pole, adult, and large adult) using a linear mixed-effects model with fire type and stage as fixed effects and random effects for the tree species and year to account for other sources of variability across fire type and stage that may affect growth. The time spent in a stage was then calculated as the average increase divided by the width of the growth class (e.g., 5 cm for poles, 25 cm for adults). Finally, the probability of a random individual transitioning up (larger) in any given year was the inverse of the time spent in that stage multiplied by the probability of increasing in dbh, where the probability of increasing in dbh was the number of trees that had a positive annual change in dbh divided by the total number of trees observed. This same procedure was repeated for trees that had a negative annual change in dbh to determine the probability of transitioning down (smaller). The

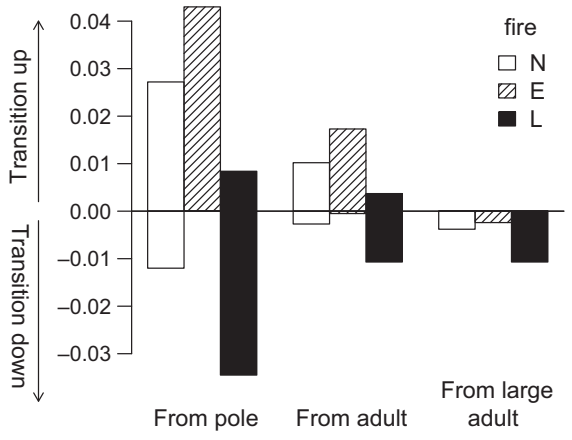

Fig. 3. Transition probabilities (per year) for poles, adults, and larger adults, calculated using growth rates in dbh on repeat measures of individual trees over 9 yr for no fire (N), early dry season fires (E), and late dry season fires (L). Details are in *Model*: *Parameterization of transition matrices.*

calculated probabilities of transitioning up or down are shown in Fig. 3.

In addition to annual changes in dbh, Werner (2005) recorded the trees that died each year, from which we calculated the probability of mortality with each fire type. In an independent study in Kapalga by Williams et al. (2003*b*), there was no relationship between adult tree survival and size (across a range ≈ 20–35 cm dbh, their Figure 6.4). The Werner (2005) data allowed us to calculate the probability of a pole, adult, or large adult surviving and remaining within the same stage (i.e., a_{ii}) as: 1 − Pr (mortality) − Pr (transition up) − Pr (transition down).

There were some instances of missing data that forced us to make three assumptions when calculating transition probabilities for mature trees (poles, adults, and large adults). Firstly, understory was not specified in the Werner (2005) study used to parameterize transition values for mature trees. In general, understory was non-sorghum or only sparse sorghum, as the plots were set up in 1982 to avoid heavy sorghum and sorghum did not enter the plots throughout the study (P. A. Werner, *unpublished* data *and photographs*). Because the type of understory likely has relatively much less effect on the survival and growth of mature trees compared to demonstrated effects on juveniles and saplings (Werner 2010), we assumed that for poles, adults, and large adults only, transition probabilities were the same for non-sorghum and sorghum understories.

The second assumption was regarding wet season fires for which transition probabilities could not be calculated directly for mature trees because sample sizes were too small—only one of these fires occurred in the plots used to parameterize values (Werner 2005). For wet season fires, we calculated transition probabilities of poles, adults, and large adults as an average of the probabilities for late dry season and early dry season fires, as the characteristics of wet season fires some qualities of both late and early dry seasons (cf. *Study system: Fires*).

The third assumption was regarding mortality rates of large adult trees (≥35 cm dbh). After early dry season fires, none of the large adults (≥35 cm dbh) in the Werner (2005) field study died, but the sample size for this stage and fire type was small (12 individuals). Although large adults are more likely to have been invaded and weakened over time by internal termite damage (piped) compared to smaller trees, Werner and Prior (2007) found no difference in survival rates between piped (hollow) and unpiped large trees under early or late dry season fires. (Should a rare, unusually intense fire or a severe storm occur, however, large trees that are heavily piped are particularly vulnerable to dying compared to unpiped trees (Lonsdale and Braithwaite 1991, Williams and Douglas 1995), two external factors not considered in our model.) On the assumption that the mortality of large adults was not truly zero even under early dry season fires, we calculated the mortality of large adults under these fires as equal to the known mortality of adults (<35 and ≥10 cm dbh) under early dry season fires, scaled by the ratio of large adult to adult mortality under unburned conditions.

We were not able to incorporate some of the demographic data from some long-term field studies (≥5 yr) that had a vegetation or landscape focus because the data were incompatible with that required to parameterize our population model (i.e., information on individual genets, especially sub-adults, and their fate with reference to other stage categories). For example, although Williams et al. (2003*b*) provided information on the survival of tagged juvenile woody

sprouts (<3 cm dbh and <3 m height), recruitment was considered the number of trees entering the stratum >3 m, as measured by changes in density of stems. Similarly, Williams et al. (1999*a*), Prior et al. (2009), and Bond et al. (2012) defined recruitment as the addition of stems into a particular size category (e.g., >5 cm dbh, the minimum size of poles in our study).

Potential biological trade-offs.—In the field data used to calculate transition rates, we explored potential biological trade-offs among growth, survival, and/or flowering. For mature trees, we found no evidence of a trade-off between growth (in dbh) in one year and the probability of survival over the next 20 yr (P. A. Werner and S. J. Peacock, *unpublished data*). Nor did we find evidence of a biological trade-off between flowering and growth (in dbh) or between flowering and survival for mature trees of these canopy eucalypts, in the absence of fires. This is true within a single year or between two adjacent years (P. A. Werner, *9 yr of unpublished data, data reported collectively in* Werner 2005).

Similarly, for sub-adults (juveniles and small saplings), there was no evidence of a biological trade-off between growth and survival (Werner and Prior 2013). Only for large saplings is the relationship between growth and survival within a year slightly negative, in some environments (cf. Werner and Franklin 2010, Werner 2012) but we did not include that possibility in our model.

Results

In this section, we present calculations of population growth rates under different fire regimes and simulations. In each case, we include both the rationale and details of specific methods and the results of various simulations.

Constant environment

Assuming a constant environment (i.e., the given fire type occurs annually, and understory type remains constant), we calculated the population growth rates and stable stage distributions for the eight transition matrices corresponding to the four fire types (N, E, L, and W) and two understories (S and NS). These serve as baseline matrices for comparisons with subsequent simulations that combine different environments. The sensitivity of population growth rates to small changes in the recruitment and transition probabilities in each of the eight transition matrices were also calculated to gain insight into the relative importance of various stages to long-term persistence of the population if those stages are altered by management or other circumstances.

Population growth rates.—For all of the fire type and understory combinations of the base matrices for constant environments, $\lambda < 1$ (i.e., the population did not persist), with two exceptions (Fig. 4). In sorghum understory, if the same fire type were to occur every year, populations of eucalypts tended to extirpation and would persist only if left unburnt. However, when left unburnt, sorghum itself does not persist (cf. *Study system: Understory*) and the understory would become unburnt non-sorghum for which $\lambda < 1$. In non-sorghum, populations of eucalypts tended to extirpation in all constant environments except under annual early dry season fires (Fig. 4). However, under annual fires, non-sorghum understory is greatly disadvantaged, and sorghum will tend to replace it (cf. *Study system: Understory*). Thus, the understory would likely become annually burnt sorghum and where

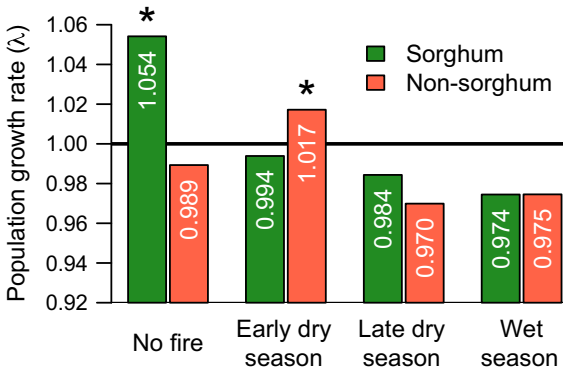

Fig. 4. The long-term population growth rates (λ; *y*-axis) under eight constant environmental conditions consisting of four fire types (*x*-axis) and sorghum understory (green) or non-sorghum understory (red). Growth rates less than 1 (horizontal black line) indicate populations that will tend toward extinction. The two environments with $\lambda > 1$ (*) are unrealistic in the long term as sorghum is not maintained in the absence of fire and is likely to replace non-sorghum under annual early dry season fires (cf. Study System: *Understory*).

$\lambda < 1$. In sum, the two exceptions to $\lambda < 1$ are unrealistic as constant environments.

Overall, the results suggest that eucalypts would not persist in a constant environment where the fire type and understory are unchanged year to year.

Stable stage distributions.—The stable stage distributions differed greatly for the eight constant environments (Fig. 5). Four fire/understory combinations had few or no seedling or juvenile stages relative to large trees (e.g., wet season fires in either understory, Fig. 5g, h; early dry season fires in sorghum, Fig. 5c; and late dry season fires in non-sorghum, Fig. 5f). In contrast, two environments showed relatively high numbers of juveniles but very few adults (e.g., unburnt non-sorghum and late dry season fires in sorghum; Fig. 5b, e). All six of these combinations of fire season and understory had $\lambda < 1$ (Table 4).

In both instances where $\lambda > 1$ under constant conditions (Fig. 4), the distribution of trees

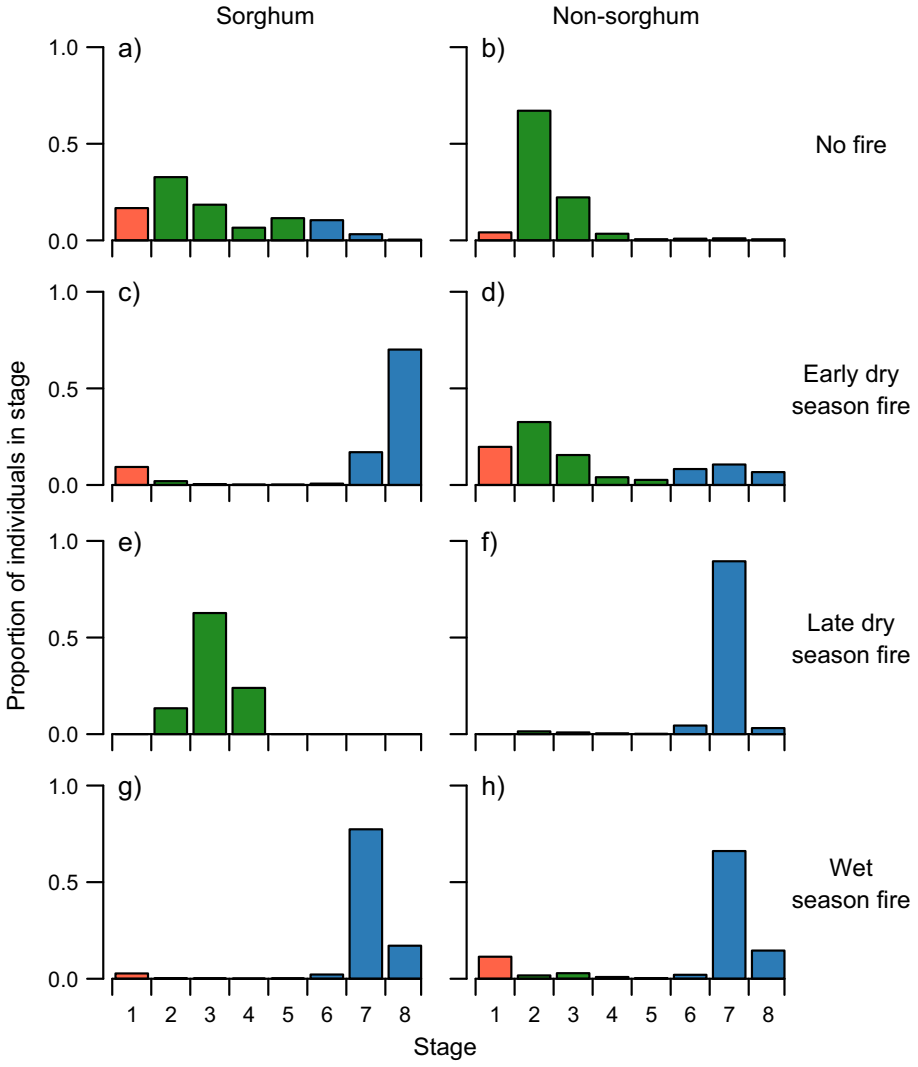

Fig. 5. Stable stage distributions (SSD) for populations growing in sorghum (left) and non-sorghum (right) understories with constant environments of no fire (a, b), early dry season fires (c, d), late dry season fires (e, f), and wet season fires (g, h). The stages are seedlings in orange, young trees (juveniles and saplings) in green, and old trees (poles and adults) in blue (Table 1). Note that populations in (a) and (d) are the only ones where $\lambda > 1$, but these are unrealistic environments in the long term (Fig. 4).

Table 4. Population growth rates λ for ten scenarios of fire seasons and return intervals in two types of understory, where the temporal sequence of fires was Deterministic (regular, periodic intervals) or Stochastic with probability of a fire in any year = 1/fire return interval, assuming zero autocorrelation in fires from year to year (Appendix S5).

Understory type	Fire season(s)	Fire return interval (yr)	Sequence of fire(s) and non-fires	Deterministic sequences λ_d	Stochastic sequences λ_s (mean ± 95% confidence interval)
Sorghum	Early dry	2	EN	0.993	1.017 (1.014, 1.020)
	Early dry	4	ENNN†	1.035	1.037 (1.034, 1.040)
	Late dry	3	LNN	0.982	0.992 (0.991, 0.993)
	Late dry	5	LNNNN	1.002	1.009 (1.008, 1.011)
	Early and late	2/5	NENEL‡	0.980	0.985 (0.982, 0.988)
Non-sorghum	Early dry	2	EN	1.005	1.011 (1.010, 1.012)
	Early dry	4	ENNN	0.999	1.002 (1.002, 1.003)
	Late dry	3	LNN	0.982	0.983 (0.982, 0.984)
	Late dry	5	LNNNN§	0.986	0.986 (0.986, 0.987)
	Early and late	2/5	NENEL	0.995	0.990 (0.988, 0.991)

† cf. Fig. 7.
‡ cf. Fig. 8.
§ cf. Fig. 9.

across stages was relatively even, or even weakly bimodal, with the greatest proportion of trees in the three smallest sizes (Fig. 6a, d). Note, however, that these two examples of constant environments are themselves unrealistic (cf. *Study system: Understory*).

Sensitivity analyses.—Overall, small changes to either recruitment into the population (seedling establishment) or the transition of seedlings to small juveniles would have negligible effect on long-term population growth rates (sensitivity values range from 0–0.02 and 0–0.08, respectively; cf. Appendix S4 for details of sensitivity analyses).

A general pattern among the eight baseline transition matrices was that the sensitivity to small changes in transition probabilities rates (cf. Appendix S4) tended to correspond to the relative abundances of various stages in the stable stage distribution (Fig. 5). Where the stable stage distributions were heavily skewed to either smaller or larger sizes (Fig. 5b, c, e–h), the sensitivity to changes in transition probabilities from those dominant stages was relatively high (0.54–1.11) but very low for transition probabilities from other stages where there were few individuals. Similarly, where the stable stage distributions were relatively evenly distributed across stages (Fig. 5a, d), there was moderate sensitivity to small changes in each of the transition probabilities (0.15–0.39).

There were also patterns related to fire and/or understory types. For example, under annual early dry season fires in sorghum, sensitivities to changes in transitions probabilities for large adults were very high (0.72–1.11) but were zero for juveniles and for saplings, a contrasting pattern to sensitivities in non-sorghum where values were lower for large adults (0.22–27) but higher for earlier life-history stages (e.g., 0.30 from small juveniles to small saplings). That pattern was reversed for late dry season fires: In sorghum, relatively high sensitivity was restricted to the early life-history stages, for example, transition rates for large juvenile trees to small sapling stage (0.66), reversions to small juvenile stage (0.54), or survival within class (0.63). This was in stark contrast to the pattern of sensitivity in non-sorghum where population growth rates were sensitive only to small changes for the late life-history stages (e.g., 0.99 for adults surviving as adults).

Under annual wet season fires, regardless of understory type, the probability of adults surviving as adults was also very important (sensitivity > 0.96), whereas changes to transition probabilities for earlier life-history stages had little or no effect on long-term population growth

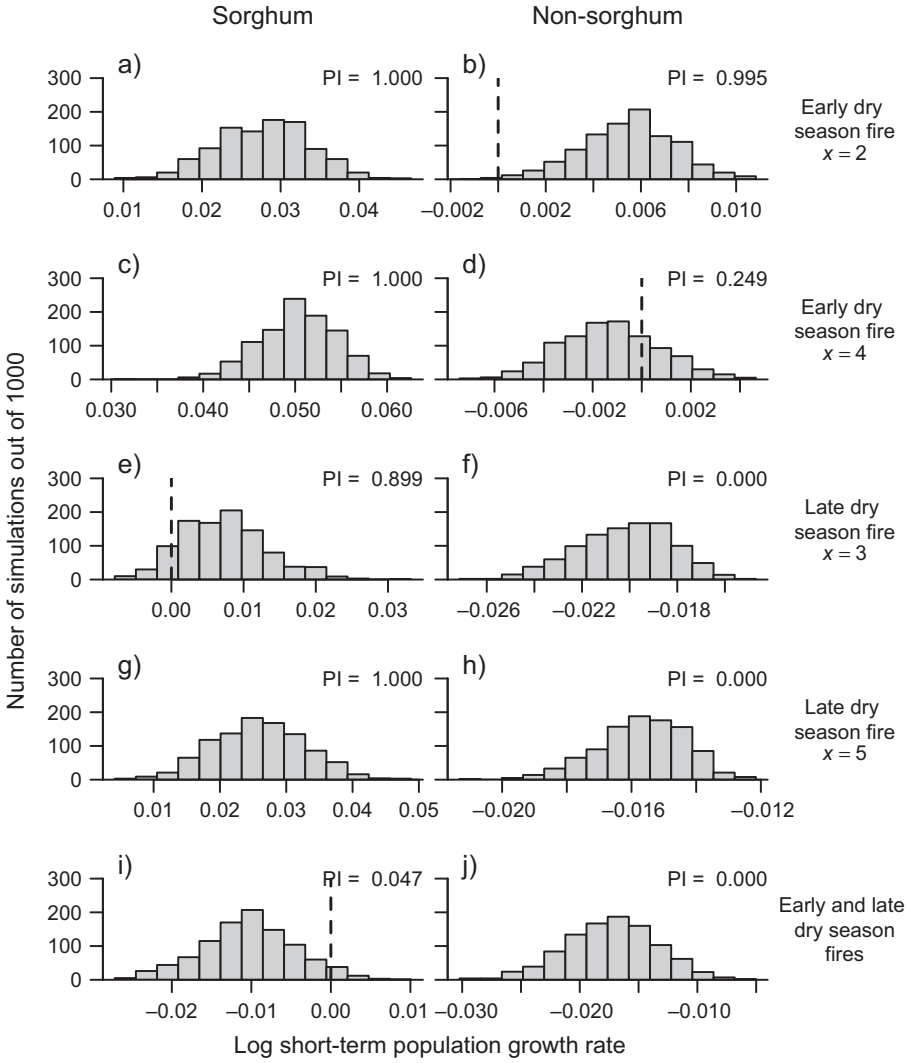

Fig. 6. The frequency distribution of the short-term population growth rates over 100 yr for 1000 independent simulations for each scenario (rows; Table 5). A vertical line is shown where the log average population growth = 0 (below which the populations are not increasing) and the proportion increasing (PI) is shown in the top-right of each panel (cf. Table 5).

rate. With no fire, sensitivity to changes in the transition probabilities of poles to the adult stage was higher in sorghum than in non-sorghum (0.59 vs. 0.26, respectively).

Variable environments

In the field, the same fire type and understory does not occur every year because the occurrence and timing of fires will vary based on management decisions, unauthorized casual ignitions, and occasional lightning strikes. Therefore, we explored the consequences of populations experiencing different fire types through time, specifically those where years of no fire are interspersed among years with fire, in both sorghum and non-sorghum understories.

The current study is limited to five different fire regimes that were chosen because they are currently and/or historically common in the north-central humid Australian savannas (Gill et al. 2000, Russell-Smith et al. 2003*a*, Russell-Smith and Edwards 2006, Murphy and Russell-

Smith 2010) and/or reflect regimes that managers aspire to, or avoid (Russell-Smith et al. 2009, 2013, Parks Australia 2016). Four of the fire regimes involved fires occurring only during one part of the dry season, but with different return intervals: early dry season fires with return intervals of two and of four years and late dry season fire with return intervals of three and of five years. The fifth fire regime incorporated both early and late dry season fires, where the early dry season fires occurred twice, the late dry season fire once, and unburnt years twice in a five-year period, on average, the most common fire regime in the region over the past several decades, including within KNP (cf. *Study system: Fires*). We considered each of these five fire regimes in sorghum and in non-sorghum understory, leading to ten different scenarios (Table 4).

The sequence of fires in each scenario was firstly considered as a deterministic process, with the same periodic sequence of fires repeated indefinitely, and then as a stochastic process, where fires occurred randomly each year based on the specified long-term frequencies of fires. For example, for the fire regime combining early (E) and late (L) dry season fires and no fires (N) over five years, the deterministic model was ENENL (Table 4), whereas the stochastic model used a corresponding 40% chance of early dry season fire, a 40% chance of no fire, and a 20% chance of late dry season fire in a given year (we did not include the possibility of multiple fires with a single year).

For the stochastic model, we assumed that there was no autocorrelation in the environment, such that the probability of a fire in any given year was independent of whether a fire had occurred the year before. Because almost all fires are set intentionally, and the frequency of fires is very high, an accumulation of fuel plays less of a role than one might expect in influencing the probability of a fire in any particular year (cf. *Study system: Fires*). Decisions to ignite fires or set fire regimes are complex, based on many factors (cf. Parks Australia 2016), and further, there are insufficient data on the sequences of fires over time to inform a model that would incorporate autocorrelations in the environment (see *General discussion: Future research*). Nonetheless, we did explore the effects of both positive and negative autocorrelation on population growth rates. For each of our ten environmental scenarios, we considered the case where the probability of each fire type depends on the previous year's fire type in a two- or three-state Markov chain. From these, we were able to incorporate temporal autocorrelation in the environment in calculations of population growth rates (details of methods and figures in Appendix S5.)

Deterministic timing of fires.—We defined the fire return interval, x, as the number of years after a fire until the landscape is burned again. For example, if a late dry season fire occurs every one out of two years, this would correspond to a fire return interval of $x = 2$. For the deterministic model, the population dynamics were simulated numerically by iterating Eq. (1) using the specified sequence of transition matrices.

The long-term population growth rate λ_d for a fire return interval of x years was calculated analytically as the xth root of the dominant eigenvalue of $\widehat{\boldsymbol{A}} = \boldsymbol{A}_L\boldsymbol{A}_N^{x-1}$ (cf. Silva et al. 1991). For the scenario considering both early and late season fires (NENEL), λ_d is the 5th root of the dominant eigenvalue of $\widehat{\boldsymbol{A}} = \boldsymbol{A}_N\boldsymbol{A}_E\boldsymbol{A}_N\boldsymbol{A}_E\boldsymbol{A}_L$. Note that the sequence of fires here influences the population dynamics and that rearranging the order of the matrices will result in different estimates of λ (cf. *Variable environments*: *Stochastic timing of fires* and Appendix S5).

In seven of the ten scenarios, the deterministic model predicted that the populations would tend to extirpation (i.e., $\lambda_d < 1$; Table 4). The fire return intervals and understory type affected whether populations would tend to decline or grow. Only in sorghum, as fire return intervals of either early or late dry season fires increased, did λ_d, moving populations from decline to growth ($\lambda_d > 1$; Table 4). In non-sorghum, the pattern was opposite, at least for fire return intervals of early dry season fires: With longer fire return intervals, λ_d decreased from 1.005 at $x = 2$ to 0.999 at $x = 4$, pushing the population from growth to decline. Late dry season fires in non-sorghum resulted in population decline. Combining early and late dry season fires resulted in population decline, regardless of understory type (Table 4).

Stochastic timing of fires.—The matrix model was also simulated stochastically such that the sequence of fires was not always the same. Each year, the transition matrix was chosen randomly and independent of the previous years,

according to the probability of each fire type (analogous to the random fire regime in Hoffmann 1999). Thus, we assumed no autocorrelation in the temporal sequence of fires (i.e., zero autocorrelation in the environment), but in Appendix S5 we explore the case with both positive and negative autocorrelation in the environment such that the probability of a fire depended on the previous year's fire type.

The long-term population growth rate in the stochastic model can be estimated only by simulation (Caswell 2001, Caswell and Kaye 2001) and was calculated as the average annual change in the population size

$$\widehat{\log \lambda_s} = \frac{1}{T}\sum_{t=1}^{T} \log\left[\frac{N(t+1)}{N(t)}\right] \quad (3)$$

where T is the length of the simulation. For the calculation of $\log \lambda_s$, we used a T that was sufficiently long enough in each case to estimate the asymptotic estimate of $\widehat{\log \lambda_s}$ and reduce the effect of the initial population size and distribution (see Appendix S5 for details and for figures of $\widehat{\log \lambda_s}$ as T increases in stochastic simulations). We calculated 95% confidence intervals (CI) on $\widehat{\log \lambda_s}$ using the formula from Caswell and Kaye (2001; also presented in Appendix S5).

To ease comparison to the deterministic results, we report the transformed values ($e^{\widehat{\log \lambda_s}} = \lambda_s$) and the 95% confidence intervals for the stochastic model (Table 4).

For nine of the ten scenarios, the population growth rate λ_s was equal or higher in the stochastic model than in the deterministic model (Table 4). In two cases of early dry season fires (every two years in sorghum and every four years in non-sorghum), populations would tend to decline under deterministic timing of fires but would tend to grow under stochastic timing of fires. In six scenarios, the 95% confidence interval for the stochastic timing of fires included the mean population growth rate for deterministic timing of fires, given the same average fire frequencies.

The higher growth rates in stochastic simulations result from longer runs of years without fires (even with no temporal autocorrelation among fires) compared to deterministic timing of fires, allowing young trees to transition up through the stages and escape the fire trap (Werner 2012). Potentially, positive temporal autocorrelation would amplify this effect by increasing the chance of long runs of years without fire. Indeed, population growth rates were always higher than cases with positive autocorrelation in fires, and conversely, negative autocorrelation (between years of fire and no fire in successive years) tended to result in lower population growth rates (cf. Appendix S5: Fig. S2). Nevertheless, our general conclusions did not change with autocorrelation in the environment (cf. Appendix S5).

Transient behavior

The previous results refer to the long-term population growth rate, but the dynamics of a population over shorter timescales (e.g., <100 yr) can be dramatically different and may be relevant to management. To capture the variability in transient dynamics for the stochastic model, we used a relatively short time period of 100 yr and ran 1000 independent simulations of the stochastic model for each scenario. For each of these simulations, we calculated the log change in population size (i.e., short-term growth rate) using equation (3) for $T = 100$ yr. (Log values were transformed for comparative purposes; cf. Variable environments: stochastic timing of fires.) We calculated the mean and the 2.5% and 97.5% quantiles (CIs) of the 1000 estimates for the short-term growth rate as well as the proportion of the 1000 simulations that had a positive change in population size (PI, proportion increasing; Table 5).

Transient dynamics are highly dependent on the initial distribution of individuals among stages (Tuljapurkar et al. 2003). We chose to initiate each simulation with a population of 1000 individuals, distributed among stages according to the stable stage distribution for early dry season fires in sorghum (Fig. 5c) and the stable stage distribution for no fire in non-sorghum (Fig. 5b). These two starting distributions were relevant because sorghum is maintained under regular early dry season fires but in long-unburnt sites, it does not persist, leaving a non-sorghum understory, and these environments tend to reflect the history of fires for each of these types of understories (cf. *Study system: Understory*). We also explored transient dynamics for

Table 5. The short-term population growth rates from the transient dynamics calculated over a 100-yr simulation starting from the stable stage distribution for early dry season fires in sorghum and the stable stage distribution for no fire in non-sorghum.

Understory type	Fire season(s)	Fire return interval (yr)	Average population growth rate† (±95% quantiles)	Proportion increasing (PI)‡
Sorghum	Early dry	2	1.028 (1.017, 1.039)	1.000
	Early dry	4	1.052 (1.043, 1.060)	1.000
	Late dry	3	1.007 (0.997, 1.021)	0.899
	Late dry	5	1.026 (1.013, 1.040)	1.000
	Early and late	2/5	0.990 (0.978, 1.001)	0.047
Non-sorghum	Early dry	2	1.005 (1.002, 1.009)	0.995
	Early dry	4	0.999 (0.995, 1.003)	0.249
	Late dry	3	0.980 (0.976, 0.983)	0.000
	Late dry	5	0.984 (0.982, 0.987)	0.000
	Early and late	2/5	0.983 (0.975, 0.990)	0.000

Notes: The temporal sequence of fires was stochastic, and simulations assumed zero autocorrelation in the environment from year to year (results using positive and negative autocorrelations are reported in Appendix S5).

† Mean (95% quantiles) of 1000 independent simulations.

‡ Proportion Increasing (PI): the proportion of the 1000 100-yr simulations where the average population growth rate was ≥1.

two other starting distributions but, for the most part, the conclusions and comparisons among fire regimes and understory types did not change (results are shown in Appendix S6: Table S1).

Population growth rates.—In sorghum understory, when fire occurred only in one season, whether early or late dry season, the average growth rate over 100 yr was greater than one with a very high proportion of the 1000 simulations resulting in population growth regardless of fire return interval (Table 5). In contrast, when a mixture of both early and late dry season fires occurred in sorghum, the mean short-term growth rate was less than one, with fewer than 5% of the 1000 simulations showing positive population growth over 100 yr (Table 5).

In non-sorghum understory, there was only one scenario (for early dry season fire at intervals of 2 yr) where the average short-term population growth rate was greater than one (with almost all of the 1000 simulations showing positive population growth), although for early dry season fires at 4-yr fire intervals the average short-term growth rate was not significantly less than one (and about a quarter of the simulations showed a positive population growth rate). In contrast, for late dry season fires or for a mixture of early and late fires in non-sorghum, the average short-term population growth rates were all less than one and none of the 1000 simulations recorded a positive population growth rate (Table 5).

Numbers of trees by stage over 100 yr.—The numbers of trees in each stage changed over the 100-yr simulations, with the biggest changes occurring over the first 60 yr. The numbers of trees in each stage also differed among the scenarios and, in some cases, between stochastic and deterministic simulations. In Appendix S6: Figs. S1–S10, we show the changes in numbers for all stages over the first 100 yr of deterministic and stochastic simulations for each of the 10 scenarios (as well as the stage distributions at 1, 30, 60, and 100 yr; below).

Here, for comparative purposes, we present results for three scenarios (of fire season, timing, and understory type) where the eucalypt populations had very different average growth rates and very different PIs.

1. *Early dry season fires with fire return intervals of four years in sorghum.*—The numbers of individuals in most stages increased exponentially over time, with the exception of large adults, which experienced an initial decline in abundance before increasing after ~40 yr. Stochastic timing of fires yielded an increasingly large range of numbers in each stage from ~60 yr onward, in general (Fig. 7).
2. *Early and late dry season fires (2- and 5-yr intervals, respectively) in sorghum.*—In contrast, when there was a mixture of early and

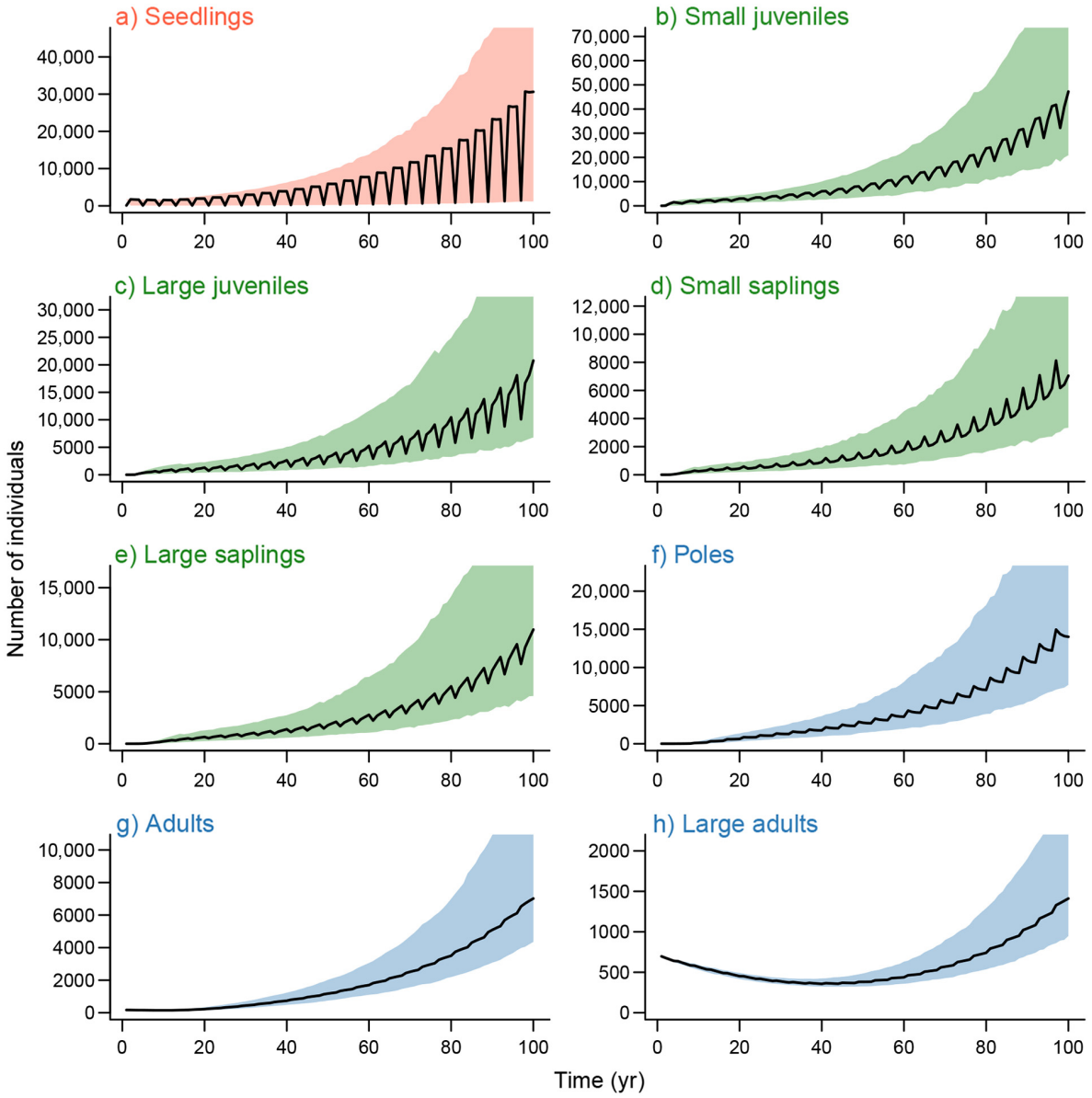

Fig. 7. Early dry season fires with fire return interval of 4 yr (ENNN) in sorghum understory: the number of individuals (y-axis) over 100 yr (x-axis) for each of 8 life-history stages (Table 1), showing the deterministic simulation (black line) and the 95% confidence intervals from 1000 stochastic simulations (shaded polygon) using the same parameters. Seedling stage in orange, juveniles and saplings in green, and poles and adults in blue.

late dry season fires, there was a steady decline in seedlings, adults, and large adults. For all other stages, there was an initial increase and then decline starting at about 20–30 yr (Fig. 8). Under stochastic timing of fires, there was a great deal of variation in numbers in each stage, often with two to three times more individuals compared to numbers under deterministic timing of fires (Fig. 8). In general, the variability in the number of individuals in each stage was much higher in scenarios that combine three fire stages (early, late, unburnt), then other scenarios which only considered two fire states (cf. Appendix S6).

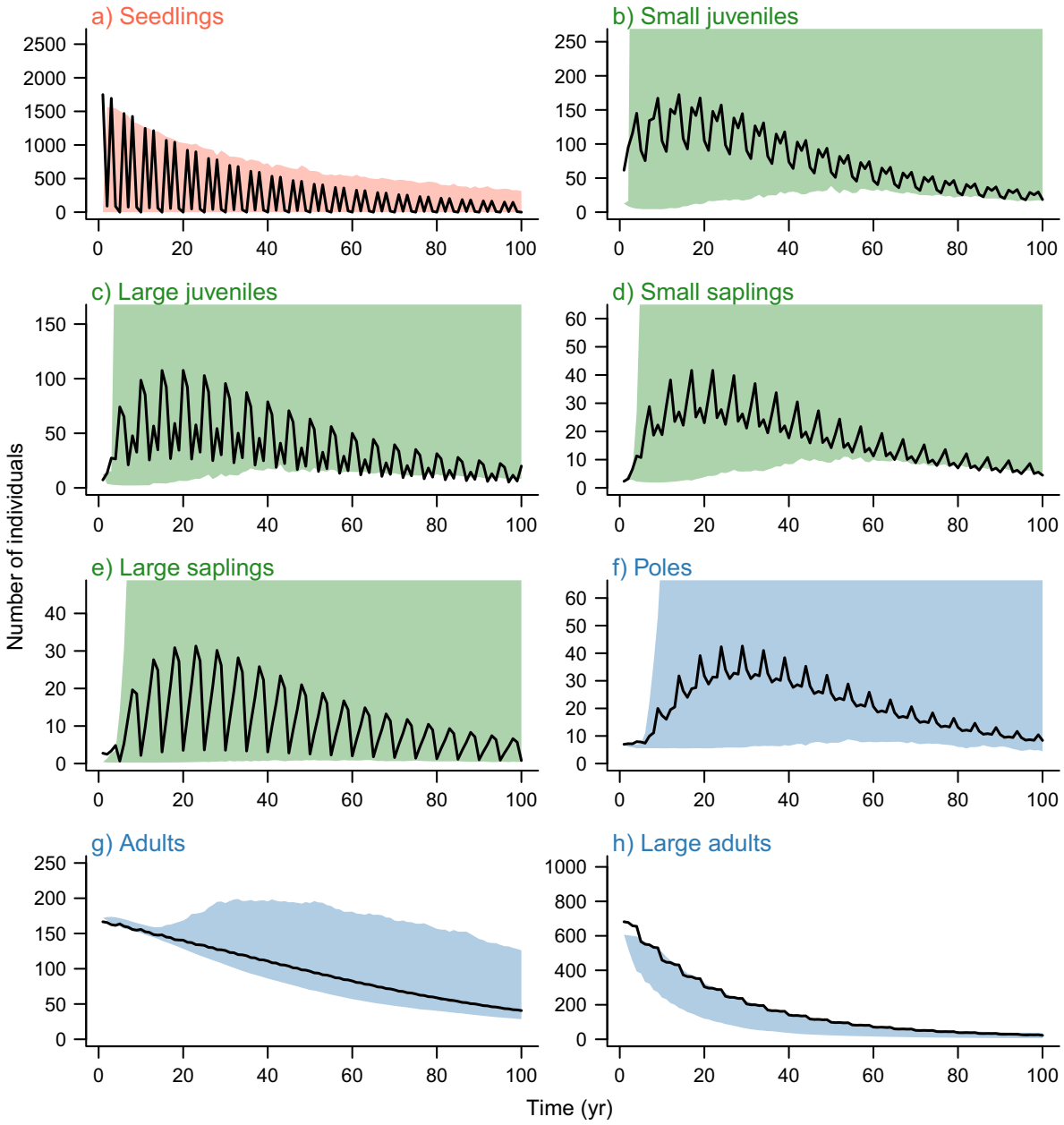

Fig. 8. A combination of early and late dry season fires with fire return intervals of 2 and 5 yr, respectively (ENENL), in sorghum understory: the number of individuals (*y*-axis) over 100 yr (*x*-axis) for each of 8 life-history stages (Table 1), showing the deterministic simulation (black line) and the 95% confidence interval from 1000 stochastic simulations (shaded polygon) using the same parameters. Colors of life-history stages as in Fig. 7.

3. *Late dry season fires with return intervals of five years in non-sorghum.*—The numbers of individuals in all stages declined over 100 yr, although poles and saplings did increase initially for about 10 yr after which numbers steadily declined (Fig. 9). Variability in numbers of trees was highest near the beginning of the simulation and then declined as all simulations had negative population growth (PI = 0; Table 5).

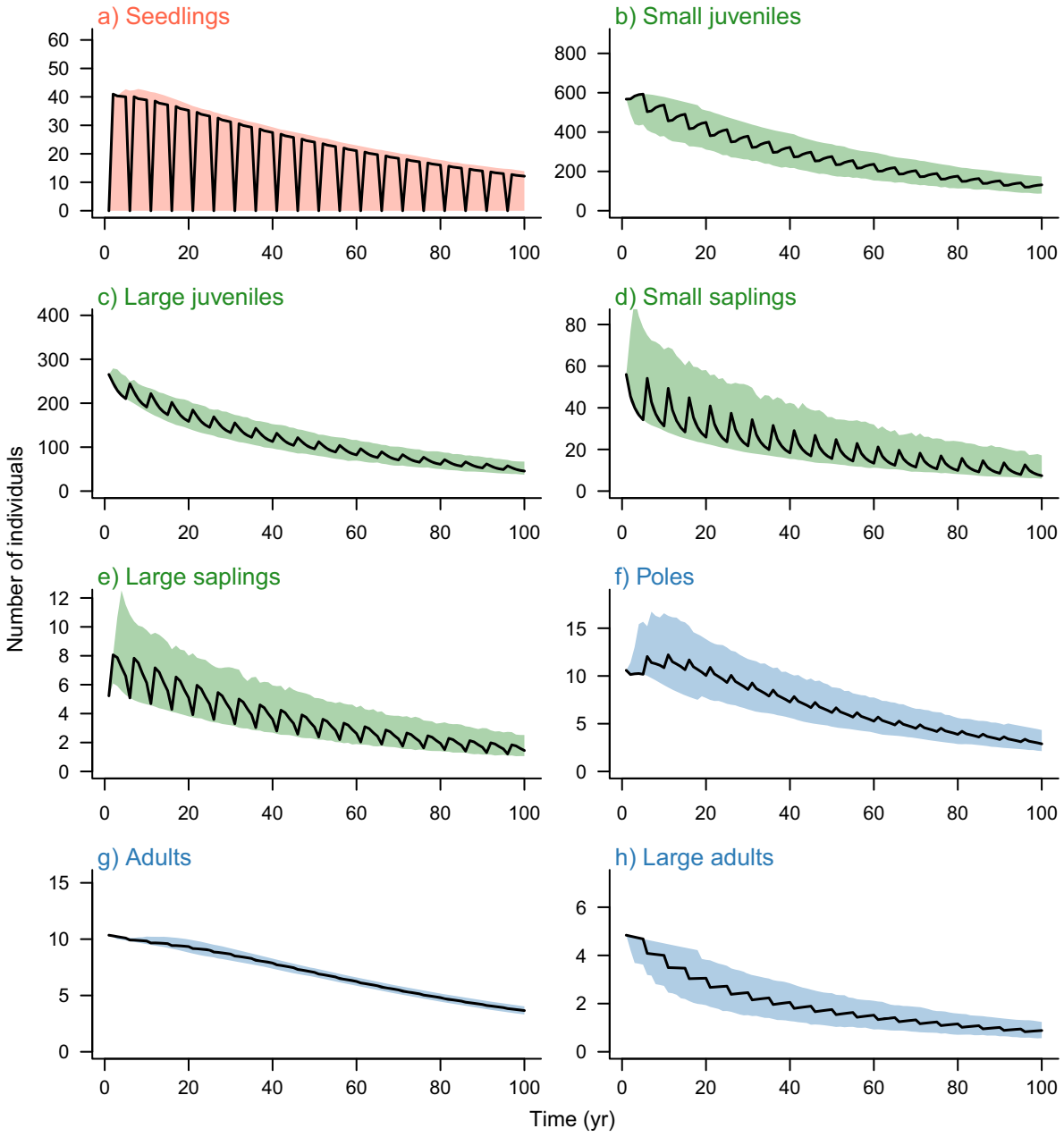

Fig. 9. Late dry season fires with fire return interval of 5 yr (LNNNN) in non-sorghum understory: the number of individuals (*y*-axis) over 100 yr (*x*-axis) for each of 8 life-history stages (Table 1), showing the deterministic simulation (black line) and the 95% confidence intervals from 1000 stochastic simulations (shaded polygon) using the same parameters. Colors of life-history stages as in Fig. 7.

Stage distributions.—The distribution of individuals among the eight stages at years 0, 30, 60, and 100 yr for each of the 10 scenarios and under stochastic timing of fires (averages of 1000 simulations) is shown in Appendix S6: Tables S11–S20). In general, changes in stage distributions occurred rather quickly, by 30 yr (in some cases by 60 yr), with little change in stage distributions thereafter. Ecologically, changes in stage distributions reflect the combined effects of

responses by various life-history stages to season of fires, timing and length of fire intervals, and understory type. Here, for purposes of comparison among fire regimes, we show the stage distributions at 100 yr for each scenario (Fig. 10).

In sorghum, under early dry season fires, the stage distributions were weakly bimodal after 100 yr. Among the early life-history stages, small juveniles were the most numerous (30–40% of the population) and poles were slightly more numerous than adult trees (Fig. 10a, c). Under late dry season fires in sorghum, the stage distributions had high numbers of juveniles, with fewer seedlings, saplings, and poles, and very few adults and large adults, an inverse J shape distribution (Fig. 10e, g). We note that for each of these three scenarios, the mean population growth rate over 100 yr was greater than one. In contrast, for a mixture of early and late dry season fires in sorghum, although the stage distribution was also weakly bimodal (Fig. 10i), the mean population rate over the 100 yr was less than one and PI was <5% (Table 5).

In non-sorghum, stage distributions were highly skewed toward small trees for all scenarios. For example, for late dry season fires with fire return intervals of five years, ~80% of the trees were juveniles (>60% small juveniles and >20% large juveniles) and relatively few of the trees were saplings or adults (Fig. 10h). Even with a highly skewed stage

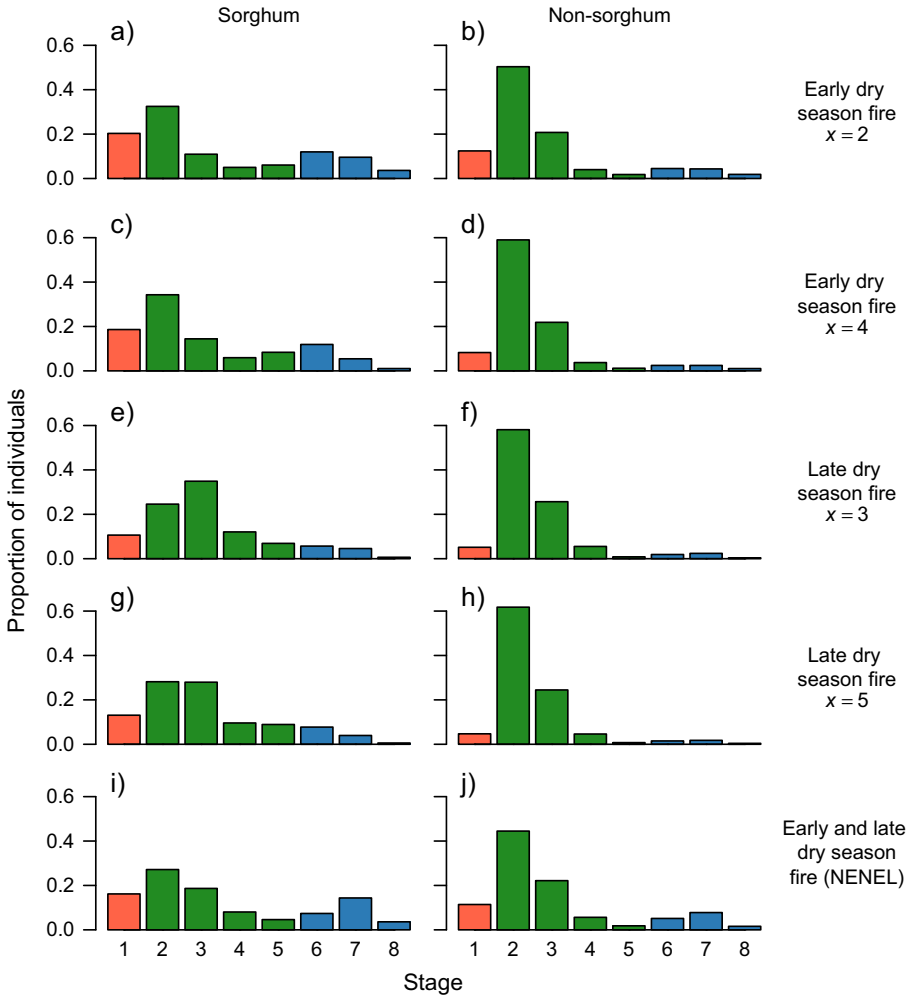

Fig. 10. The distribution of individuals among the eight stages after 100 yr for stochastic simulations under five fire regimes (rows) in sorghum and non-sorghum (columns).

distribution favoring small trees (Fig. 10b, d), mean population growth was greater than one for early dry season fires alone, but for all scenarios that include late dry season fires in non-sorghum, short-term growth rates were <1 (Table 5).

Model Test: Predicting Population Dynamics in KNP, 1982–2003

A unique opportunity to test the predictions of our model against field data was provided by a long-term monitoring study of 528 individually marked eucalyptus trees located in four relatively isolated sites in Kapalga Research Station in KNP. The fire history of each site was recorded annually for 22 yr from 1982 to 2003, by ground observation for first nine years and by ground observations and satellite imagery for the next 13 yr (Werner 2005; cf. Appendix S7: Table S1). The type of understory was not always recorded but was known to be non-sorghum in these sites at the start of the study in 1982 (P. A. Werner, *photographs*).

The initial numbers of small saplings, large saplings, poles, adults, and large adults used for the model test were derived from the number and sizes of trees permanently marked and initially measured in October 1982 in five plots in each of four sites: known as 4S, 4N, 3S, 3N, for a total area of 1.8 km^2 (previously *unpublished data* by stage but reported collectively in Werner 2005). We used these initial field counts from October but kept our census time in January because there were no fires between October 1982 and January 1983, when the same trees were monitored for survival and growth. Further, quarterly monitoring for the next 16 months indicated that no trees died and that between October and January growth was negligible, being the end of the dry season (P. A. Werner, *unpublished data*). Seedlings and juvenile trees were counted in 120 belt transects totaling 655 m^2 within the four sites in January 1983 and were monitored annually for six years; 23 eucalypt juveniles were recorded in the initial census and another 35 eucalypt small juveniles became established over the next five years (Werner et al. 2006). No seedlings were recorded in any of the transects in January 1983, which is corroborated by field data indicating that the rates of flowering and fruiting by mature trees within the sites were extremely low (6% and <1%, respectively) in 1982 (P. A. Werner and J. S. Cusack, *unpublished data*). By adjusting these initial data to a common areal scale (per hectare), we estimated an initial stage distribution for each of the four sites in January 1983 (cf. Appendix S7: Table S2).

From the 1983 initial stage distribution in each site, we iterated equation (1) (cf. Model: *General model form*) to simulate the population dynamics over the next 21 yr, ending in 2003. Simulations were run separately for each of the four sites (4S, 4N, 3S, and 3N) because fire history differed among sites (Appendix S1: Table S5.1). We also determined the population growth rate over the 21-yr simulation for each site, calculated as the dominant eigenvalue of the product of the transition matrices over the 21 yr, raised to the power of 1/21. Populations showed overall positive growth over the 21-yr simulation in all four sites, with short-term population growth rates greater than one: 1.015 (4S), 1.012 (4N), 1.000 (3S), and 1.011 (3N).

For site 4S, we show the predicted numbers of trees in each stage over 21 yr, the actual numbers of saplings and mature trees in 1989 and 2003, and the fire history by year (Fig. 11). A composite figure of results for all four sites is shown in Appendix S7: Fig. S1, as well as the results for each of the four sites in Appendix S7: Figs. S2–S5. The predicted numbers of seedlings showed high interannual variability due to the strong dependency on fire type. For example, the pulse of seedlings that progressed to large juveniles from 1984 to 1989 in site 4S was the result of four consecutive years without fire in this site, which allowed relatively high recruitment and survival of seedlings over that time (Fig. 11). Field data over time for seedlings and juveniles were not available to verify those aspects of model predictions.

The model tended to overpredict the numbers of small saplings in 1989 and in 2003 but was much better at estimating the number of large saplings on all four sites (Fig. 11; cf. Appendix S7: Fig. S1). Because the fate of smaller trees influences the number of larger trees, overall, these results suggest that our model underestimates mortality of seedlings and juveniles and overestimates mortality of small saplings.

The predicted number of poles initially increased over time in site 4S as well as in the other 3 sites, but then declined quite sharply after ~14 yr (as did saplings in several sites; Fig. 11; cf.

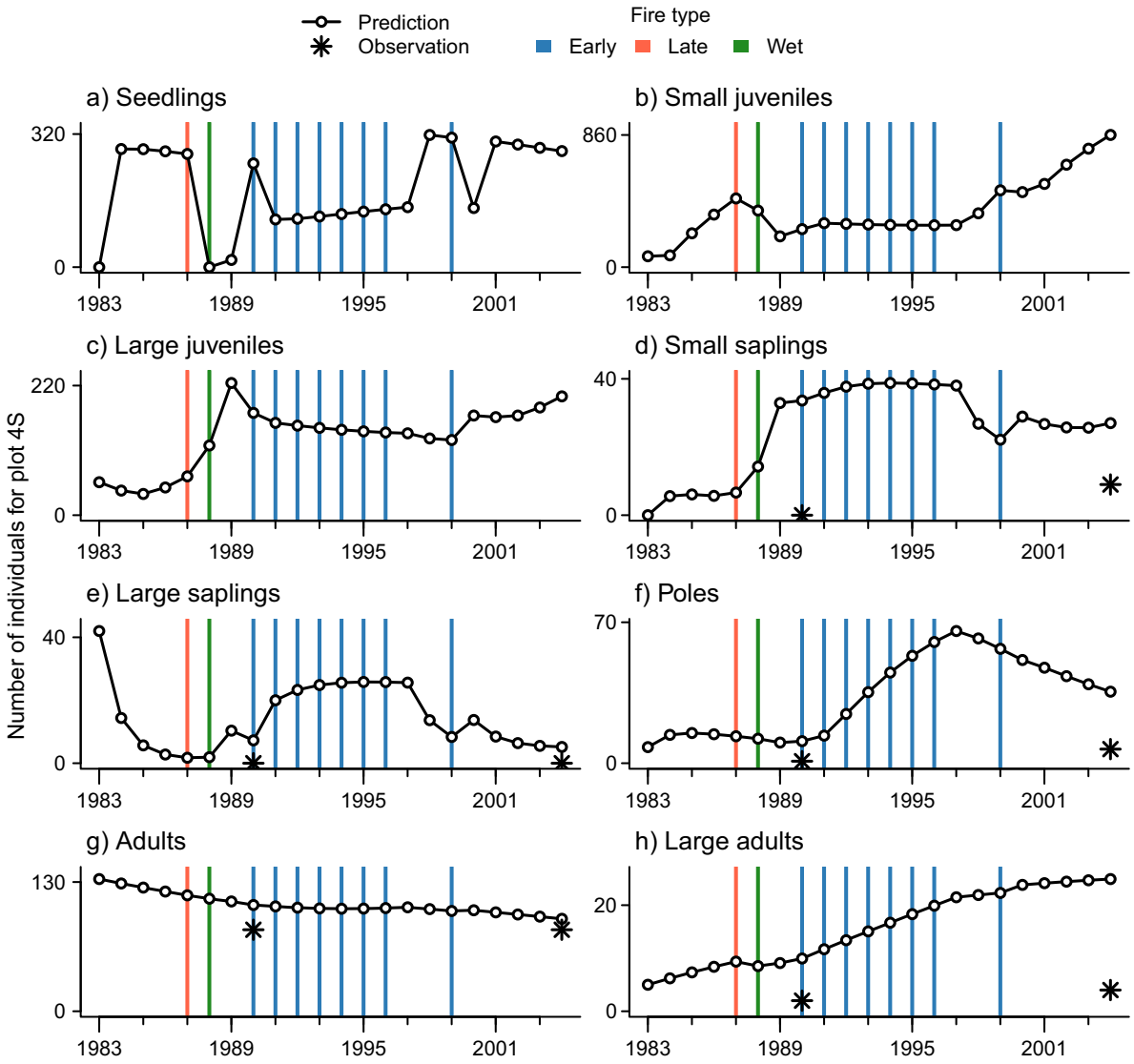

Fig. 11. For Site 4S in Kapalga, Kakadu National Park, the predicted number of individuals in each stage (a–h; Table 1) over time, from simulations starting with the known stage distribution in January 1983 (Appendix S7: Table S2) and calculated for the next 21 yr, using the known sequence of fires (Appendix S7: Table S1): early dry season fires (vertical blue lines), late dry season fires (vertical red lines), and one wet season fire (vertical green line). The number of trees counted in the field in October 1989 and 2003 is shown as stars in panels (d–h).

Appendix S7: Fig. S1). Because the projected shift from increasing to decreasing number of poles (as well as a similar shift from increasing to decreasing number of large and small saplings) occurred mainly between the two later census years (1989 and 2003), the precise timing of that shift could not be verified from field data. Overall, the predicted numbers of poles were overestimated for 1989 and 2003 when compared to field data. Both the overestimate of poles and the rapid drop in both poles and saplings after ~1996 were particularly evident in site 4S, occurring after a series of seven annual early dry season fires followed by a period with few fires (Fig. 11).

The predicted number of adult trees steadily declined over the entire 21 yr whereas very large

adult trees steadily increased over the same period, in all four sites. Field data in 2003 confirmed projected declines in the number of adult trees (less so in 1989), with the magnitude of declines slightly less than the projected levels. For very large trees, there were many fewer than had been projected by the model (Fig. 11; cf. Appendix S7: Figs. S2–S5).

Discrepancies between model predictions and field data for 1989 and 2003 in these four sites may stem from the paucity of data available for estimates of the initial numbers for seedling and juvenile stages in 1983 as well as two environmental factors not included in our model: a potential historical effect of feral Asian water buffalo on survival of juvenile trees in the early years, and a potential storm selectively decimating the largest trees. These are discussed further in Appendix S7.

Despite these discrepancies, the proportion of variance between predicted and actual tree numbers (small saplings, large saplings, poles, adults, and large adults) explained by the model was high (r^2 = 0.880; Fig. 12).

Overall, the model performs well for the population and in environments experienced in typical eucalyptus open forest at Kapalga, KNP. This provides confidence that projections calculated by the population model and analyses of transient behavior of the canopy trees can yield valuable insights into the mechanisms underpinning population dynamics of those savanna open forests that have a similar soil/precipitation/productivity profiles in the larger Australian humid savannas.

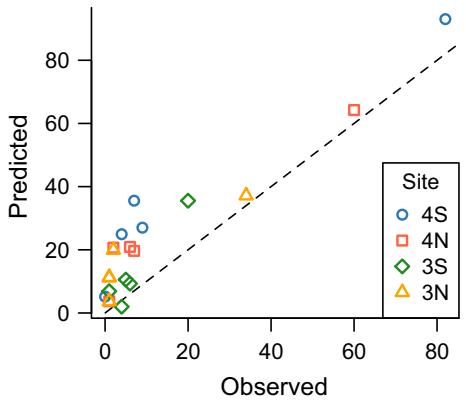

Fig. 12. The model-predicted number of trees compared to the observed number of trees in the five largest stages (small saplings, large saplings, poles, adults, and large adults) for each of the four sites surveyed in 2003 in Kapalga, Kakadu National Park. The dashed line shows the 1:1 relationship indicating perfect correspondence, and the proportion of variance in the observations explained by the model is R^2 = 0.880.

Discussion

Strengths of the population modeling approach

This study provides the first comprehensive analysis of field data on the response of all life-history stages (including the usually elusive early life-history stages) of canopy trees in the savannas of northern Australia to key environmental factors. We integrated this information on tree behaviors in a stage-based population model that focused on the combined impact of to two key environmental factors—fire and understory—on canopy tree population dynamics. In effect, the approach integrates individual tree behaviors into a model that projects those behaviors into system outcomes. The modeling approach is able to provide valuable insights into the dynamics of the savanna system (the how) rather than attempting to discern mechanisms from analyses of pattern (the what).

Relatively simple models of population dynamics such as ours undoubtedly ignore some realities of the environment but can nonetheless provide clarity and insights into the major factors influencing population change (Brook et al. 2002). Most other modeling studies on the effects of fire in savanna ecosystems have adopted simulation-based approaches using highly mechanistic sub-models describing the response of plants to their environment. Simulation-based approaches can provide accurate predictions under specific scenarios and parameterizations, but the output may depend strongly on initial conditions and the many parameters that require detailed data. For example, in Australian savannas, the widely used process-based, empirical computer simulation model (FLAMES) is implemented on a spatial grid of stem counts that requires historical rainfall, soil properties, and vegetation characteristics for each grid cell (cf. Liedloff and Cook 2007). Another example that requires even more specific data is the

TREEGRASS model of Simioni et al. (2000) in northwest African savannas which is initiated with the position and orientation of each tree in the population, and simulates physiological processes controlling growth at the individual level on an hourly timescale.

Detailed mechanistic process models are very well suited for robust predictions of stand-level descriptions (e.g., biomass, tree–grass ratios, woody plant size structures) and how these change across environmental gradients (e.g., precipitation, soils, fire frequency) and can inform specific management actions. On the other hand, the complexity of multiple, mechanistic submodels and sensitivity to initial conditions often can make it difficult to understand the ecological mechanisms and primary drivers of the observed dynamics in these models.

The aim of our population modeling approach was to develop an understanding of how fire affects canopy tree populations and to provide generalizable methods and insights into system dynamics. A more thorough discussion of the strengths and limitation of our model, as well as an examination of two basic assumptions, is presented in Appendix S3. The model is suited to future modifications of the transition matrices and can be extended to include other environmental factors, as described in Appendix S8.

Key findings

Fire is necessary for long-term persistence.—We found that eucalypt canopy populations would not persist if left unburnt, which is consistent with independent field studies where fire was intentionally suppressed in the long-monitored field locations in north-central Australia. For example, in unburnt plots in both Solar Village (Woinarski et al. 2004) and Territory Wildlife Park (Scott et al. 2012) southeast of Darwin, the eucalypts that usually dominate in open forest canopies declined significantly over a few decades and other, fire-sensitive, shorter-statured tree and shrub species increased, intermingled with larger, previously established eucalypt trees. Few eucalyptus saplings were found in the long-unburnt plots in either of these sites, as well as in the treatment plots where fire was suppressed in the 23 yr long experimental site at Munmarlary (now part of KNP; Bowman et al. 1988, Russell-Smith et al. 2003*b*).

Population responses of fire-sensitive species can be very rapid compared to responses by fire-resilient species. For example, when fire was re-introduced into a portion of Territory Wildlife Park after 20 yr of deliberate fire exclusion, the fire-sensitive woody species, regardless of size, tended to disappear quickly and, among trees, only the larger established fire-resilient eucalypt trees survived (Scott et al. 2012). The reverse occurred in Kapalga (KNP), where plots that had experienced annual early dry season fires were then intentionally left unburnt; a eucalyptus sapling bottleneck quickly developed with 20–50% of eucalyptus saplings losing height and 45% of pole-sizes trees dying in just three years (Werner and Franklin 2010, Werner 2012).

The dominant tree canopy of the mesic pine savannas of southeastern United States also depends on fire. At sites where fire was excluded for 80 yr, seedlings and saplings of the usual dominant canopy species, *Pinus palustris*, were very rare but those of the fire-sensitive oak species were very high. This contrasted with the larger areas where fires occurred at regular intervals and where oaks were replaced by fire-resistant pine trees, the common dominant canopy tree in those savannas (Gilliam and Platt 1999, Gilliam et al. 2006). In both North American and Australian savannas, fire-sensitive tree species were able to outcompete fire-resistant tree species in the absence of fire. As a result, the most common dominant canopy species, indeed, the colloquial names for these savannas (pine savanna and eucalypt open forest), are a product of the fires that have removed competitors.

Our finding that canopy tree populations require fire to persist suggests that the vast eucalypt-dominated savannas of northern Australia are most likely anthropogenic landscapes, the result of tens of thousands of years of indigenous occupation and burning of vegetation (cf. *Discussion: Implications for savanna physiognomy*).

Annual fires are not conducive to long-term persistence.—Populations of the canopy eucalypts would tend to decline when fires occur annually, regardless of the season of fire. Ecologically, this is most likely due to the severe effect that any fire has on seedling establishment and survival, as

well as on growth of juvenile trees (difficulty reaching sapling size) that leads to the demographic bottlenecks described in savannas on three continents (Werner 2012, Grady and Hoffmann 2012, Clarke et al. 2012, Holdo et al. 2014).

From a five-year study of annual fires, Andersen et al. (2003*b*) suggested that substantial fire-free intervals (>3 yr) would be required for effective juvenile tree recruitment. When fires occur every year, there is very little opportunity for young trees to grow to a size that allows escape from the fire trap (Werner 2012). Inability to bridge the fire trap over long periods of time would have severe population consequences: As mature trees die off, recruitment ceases, and ultimately the population would be extirpated, the result projected by our model.

Fire season and frequency determine population persistence.—Periodic fires were required to sustain a population, but not all fire regimes promoted long-term persistence. In general, periodic, early dry season fires were more likely to promote long-term persistence of eucalyptus populations than were periodic, late dry season fires, and recurring mixtures of the two fire seasons were particularly detrimental. This is most likely the result of both the inherent patchiness of burn patterns of early dry season fires, and their more benign effects on tree recruitment, seedlings, juvenile and sapling survival and growth compared to the more severe effects of late dry season fires, especially on saplings (and as reflected in the transition matrices of Table 3).

Further, longer fire return intervals (within the range that we explored) tended to be more advantageous to population growth rates compared to shorter fire return intervals. This pattern was particularly evident in sorghum understory, but much less so in non-sorghum understory where, in some cases, shorter fire return intervals were more conducive to population growth. The advantage of longer fire return intervals is related to the length of time individual plants would have the opportunity to escape fire but mitigated by the greater competitive effect of non-sorghum understory on juvenile trees compared to sorghum understory.

Finally, we found that the mixture of early and late dry season fires was extremely detrimental to long-term persistence as well as to transient dynamics. This result is particularly relevant because it has been the most common contemporary fire history in the region, including in protected areas such as KNP (*cf. Study system: Fires*).

Irregular timing of fires promotes persistence.—The most consistent result across all scenarios modeled was that stochastic timing of fires favored persistence over deterministic timing of fires within comparable fire regimes (Table 4). This was generally true regardless of whether environmental autocorrelations were incorporated into calculations (cf. Appendix S5). When the timing of fires is stochastic, there is a greater chance of multiple, consecutive fire-free years that allow small trees to transition into larger size categories instead of being top-killed. As larger trees, the probability of their surviving subsequent fires is higher, and they are more likely to grow to contribute to recruitment within the population. This was especially evident in cases where the mean long-term growth rate under deterministic timing of fire indicated a trajectory toward extinction: When timing of fires was stochastic, the increased possibility of several consecutive fire-free years resulted in positive population growth (e.g., EN in sorghum, Table 4).

The positive effect of stochastic timing of fire has also been reported for woody species in cerrado of Brazil, where a random fire regime produced higher population growth rates than did fixed intervals of fires (Hoffmann 1999). The random fires in that study were simulated in the same way as our stochastic simulations, and the result was the same: Fires set on a regular schedule lead to lower long-term population growth of trees in both Brazilian cerrado and Australian humid savannas.

Understory type influences tree population dynamics.—Canopy trees have different population dynamics in sorghum and non-sorghum understories. Ecologically, these differences are not unexpected. Sorghum understory has less competitive effect on the survival and growth of small eucalyptus trees than does non-sorghum understory due to differences in phenology and shading. Alternatively, in sorghum, the late dry season fires are particularly detrimental to survival of saplings (cf. *Study system: Understory*). To illustrate this point, using field data on large saplings in late dry season fires, in sorghum understory 60% of the saplings were reduced to

juvenile height and 20% died whereas, in non-sorghum, 60% of the saplings grew to larger sizes and none died (Werner 2012).

This finding highlights the need to consider the ecological context of fire effects on savanna tree populations. It is particularly relevant to management because understory type can be changed in response to management decisions, which in turn can alter the impact of subsequent fires on tree populations (cf. Discussion: *Implications for management*).

Transient dynamics uphold key findings.—The transient dynamics over 100 yr tended to reflect the key findings for long-term population growth with respect to the role of fire regimes and understory on population growth rates. Specifically, population growth rates over 100 yr were higher with early dry season fires compared to late dry season fires or mixtures of the two seasons, in sorghum understory compared to non-sorghum understory, and with stochastic timing of fires compared to deterministic timing of fires. Within scenarios, the average population growth rates over the first 100 yr were generally higher than the long-term population growth rates, most likely due to the continued survival of very large trees over the 100 yr. Nonetheless, the similar conclusions drawn from long- and short-term dynamics suggest that our key finding may be generalizable to different initial conditions.

Stage distributions can change rapidly.—Over 100 yr of transient dynamics, changes in stage distributions (proportional numbers within each of the eight stages) occurred rather quickly, with greatest changes occurring in the initial 30 yr of simulations. Ecologically, the combined effects of responses by various life-history stages to season of fires, timing and length of fire intervals, and understory type interact in such a way to result in changes on rather short time scales relative to the life span of an individual tree; such a degree and rate of change in savanna structure can have profound effects on other biota (cf. *Discussion*: *Implications for savanna physiognomy*).

After 100 yr under various fire regimes, the tree populations in sorghum understory often exhibited a bimodal distribution such as found in some disturbance-driven populations (Balke et al. 2014), or a weak inverse J shape distribution usually found in age-classified, steadily growing or stable populations (Caswell 2001). All but one of the fire regimes in sorghum had a short-term population growth rate greater than one. In contrast, in non-sorghum understory, stage distributions were very strongly inverse J shaped (~80% of individuals were juveniles), and in all but one case, mean population growth rates were <1.

Recruitment and seedling survival are relatively unimportant.—In the open forest eucalypt populations of north-central Australian humid savannas, small changes to vital rates for recruitment or seedling survival would have relatively little effect on the potential for long-term persistence, compared to small changes in other vital rates. This is based on the very low sensitivity values calculated for all the fire seasons and understory types we considered (cf. Appendix S4). In any case, in the field, the production seeds and seedlings and survival of seedlings of these tree species are extremely low (cf. Appendix S2). Simulated increases in seedling establishment by five times and survival of seedlings by two times made little difference to population growth (P. A. Werner and S. J. Peacock, *unpublished analyses*).

Similarly, Hoffmann (1999) found that sexual reproduction contributed little to the overall effect of fire on calculated population growth rates of two trees and two shrub species in the cerrado savanna of Brazil. In reviews of population growth rates for scores of woody plant species, Silvertown et al. (1993) and Pfister (1998) concluded that changes in fecundity were of relatively low importance, compared to changes in growth or survival of the established plants. Further, Franco and Silvertown (2004) compared population dynamics of 102 perennial plants and concluded that, in general, for long-lived species, long-term growth rates are relatively insensitive to changes in seed production.

In drier savannas elsewhere in Australia, the role of recruitment and seedling survival may be relatively more important than in the humid savannas of our study (Fensham et al. 2017). In all Australian savannas, tree seedlings are rare and appear only after the first rains; however, in the semi-arid savannas, several years can pass without a wet season whereas in the humid savannas, wet season rains occur every year. In the humid savannas, it is the highly variable fire regimes—and their direct effects on juveniles,

saplings, and larger trees—that is the primary factor influencing population dynamics of the canopy trees.

Implications for savanna physiognomy

Researchers on every continent have called for more information on life histories and population dynamics of savanna trees to improve theory of savanna structure (physiognomy) and function (House et al. 2003, Sankaran 2005, Midgley et al. 2010, Lehmann et al. 2014). By substituting space for time, some field studies or reviews of the Australian humid savannas have concluded that disturbance (e.g., fire and/or storms and/or grazing) is indeed an important driver that explains savanna physiognomy (e.g., different degrees of woody cover and/or size distributions of larger trees; e.g., Petty et al. 2007, Prior et al. 2006, 2009, Lehmann et al. 2009, Murphy et al. 2014). A basic understanding of the ecological mechanisms, however, has been more elusive; for example, Lehmann et al. (2009) ignored juvenile stages entirely (Midgley et al. 2010). We have contributed to a general understanding of mechanisms responsible for savanna structure (physiognomy) in the Australian humid savannas by integrating life histories of the canopy trees and their field-based responses to fire into a population model.

Among the fire regimes that we examined where populations of canopy trees were most likely to be expiated, the length of time for total exclusion to occur would be more than a century and up to the maximum life span of an established eucalypt tree, estimated at 150–300 yr (Werner 1986, Cook et al. 2005). Nevertheless, population stage structures can change rapidly certainly within the first 30 yr as shown in figures of stage distributions (cf. Appendix S6). A rapid shift in structure is consistent with independent field studies after fire regimes have been modified. For example, stage structures of eucalypts changed rapidly after fire was re-introduced to experimental sites that had been long protected from fires (Woinarski et al. 2004, Scott et al. 2012). Further, in Kapalga in KNP, under newly imposed annual late dry season fires, site total basal area (BA) of woody plants declined over just a five-year period, attributed to deaths of the largest trees without an equivalent increase in the total BA of small trees (Williams 2003b). These results suggest that many different stage distributions (and hence, vegetation structure, or physiognomy) may exist across the humid savannas of Australia, given the rapid and dynamic nature of changes in human settlements, land tenure, and fire management over the past half century.

Similarly, in pine savanna in SE United States, a range of different size structures has been found among various stands of the dominant canopy trees. This has been attributed to the combined effect of both short-term disturbance (e.g., fire) and long-term disturbance (e.g., hurricanes) on various stages in the life cycle of the trees (Platt et al. 1988, 2002, Gilliam et al. 2006). The question remains as to what extent these various stage distributions in the field, in either pine savannas or eucalypt savannas, represent stages in a cyclical pattern of responses to disturbance and/or represent a longer-term trajectory of change (cf. Appendix S8).

Some recent reviews on Australian savannas have concluded that fire regimes are either of secondary importance or unimportant compared to precipitation and/or soils in explaining vegetation structure, woody biomass, woody stem density, total basal area, and/or carbon stocks or sequestration (cf. Liedloff and Cook 2007, Murphy et al. 2015 and references therein). However, these conclusions are based on comparisons of sites across regional, sub-continental, or geological scales and so it is not surprising that abiotic factors would be the major factor accounting for differences in ecosystem characteristics across these larger geographic scales. At a finer geographical scale (e.g., within a specified area of common precipitation and soils), however, fire has been identified as the key factor affecting plant population dynamics, population size structures, and savanna physiognomy. These include results from a myriad of field studies (cited above and references therein), and from our population model (Tables 4, 5; Appendix S6: Figs. S1–S20), and from aspects and extensions of the FLAMES process-based model (e.g., site woody stem density; Liedloff and Cook 2007, Liedloff and Smith 2010).

Anthropological landscapes.—The open forests and other wooded savannas of northern Australia are anthropological landscapes. The canopy tree populations require fire for long-

term persistence and almost all (~95% of the burnt areas) are the result of fires set by humans. An anthropological landscape undoubtedly has been the case for tens of thousands of years—perhaps as much as >50,000 yr when humans first entered the continent. Our knowledge of traditional fire management comes from oral history, archeological studies, early explorers, and contemporary peoples living on the land (cf. Yibarbuk et al. 2001). Traditional practices continued to be most common until ~75 yr ago in the Alligator Rivers Area and Arnhem Land (Haynes 1985). These practices were slowly overtaken by contemporary practices in most of these areas only in the last 50 yr.

Prior to modern times, thousands of indigenous people lived on the land in north-central Australia, carrying and using fire as they moved across the landscape, hunting and gathering food and other resources. They lit fires as they walked, for several reasons: to assist in these endeavors, as well as to provide easier or safer passage, to protect campsites, and to fulfill traditional obligations to "care for country" or "clean up country" (comments by W. Roberts, *personal communication*, 1984). The many fires lit in the early dry season created patches of burnt ground (cf. *Study system*: *Fires*), with the effect of producing in a mosaic of fire breaks that reduced the spread of later late dry season or lightning-ignited fires in the following early wet season. In the first part of a dry season, hunting, collecting, and fires occurred on the ridges and high ground, where open forests are found. As the dry season progressed, activities moved downslope to lower ground eventually to include the vast floodplains of major rivers. This pattern of fire progression has continued to modern times (P. A. Werner, *personal observation*, 1981–1984). Certain areas were always protected from fires, such as the "sacred" monsoon rainforests, seeps, and smaller river beds.

The >50,000-yr history of human-set fires that produced an anthropological landscape in northern Australia is in contrast with the savannas of the SE United States coastal plain. There, lightning strikes are some of highest rates in the world, and lightning-set fires are credited with both the evolution and maintenance of the pine savannas of that region (Peet et al. 2018). In the Australian open forests, the largest adult trees alive today became established under traditional fire regimes—they are remnants of traditional fire management by indigenous peoples.

As projected by our study, recent contemporary fire regimes in the open forests of humid savannas in Australia are not conducive to long-term persistence of the canopy tree population. Should very high-frequency fire regimes lit by humans continue, areas burnt by lightning-set fires will certainly continue to be rare due to reduced fuel loads (cf. *Study system*: *Fires*), but the canopy tree populations would be slowly extirpated. Of course, the replacement—grassy savannas—would also be (modern) anthropological landscapes.

Implications for management

The lowland open forests of north-central Australia are generally considered relative intact by local managers of the region (although may be subject to decline; e.g., Russell-Smith et al. 2013, Parks Australia 2016). The current plan of management for KNP (2016–2026; Parks Australia 2016), in the section dealing with habitats of concern, is silent on potential threats to the open forests which cover more than half of the terrestrial area of the Park.

The results of our modeling, however, portend a different story: That a canopy tree population experiencing the most common fire regimes of recent decades (very high frequency of both early and late dry season fires) will most likely be driven to extirpation. Perhaps the difference between the current perceived status and the projected status is due to the presence of the large trees that continue to dominate the landscape, perhaps giving a false sense of well-being. The largest trees were established more than 50–150 yr ago, before contemporary influences (including fire management) on the open forests (cf. *Study system: Site overview*). Further, little attention has been paid to the potential replacement of those large trees when they become senescent and die, whereas our work has incorporated the early life-history stages into the predictive models.

Of necessity, management planning regarding fire in most areas of these savannas is made on a landscape scale (areal or gross scale). The vast size, distance to settlements and roads, and low density of humans result in management by fire

that is less about fire control than it is about decisions on when and where to set ignitions. Decisions are driven by social and cultural issues, time and resources available, and economic and feasibility factors (e.g., in Kakadu National Park; Parks Australia 2016).

There is widespread agreement in the entire region that late dry season fires are to be avoided because a single fire that time of year can burn very large areas (>1000 km^2), threaten humans and fauna, and devastate fire-sensitive plant species, many of which occur naturally in the understory. More recently, the areal extent and severity of late dry season fires have been identified as a major factor in the decline of small mammals regionally and in other fauna recorded in KNP over the past 30 yr (Woinarski et al. 2001, Woinarski 2011, Lawes et al. 2015) due to secondary changes in food supply, habitat, and exposure to predators. (But note that from population viability analyses (PVA) modeling fire frequency was a higher risk than fire size for small mammals; Griffiths et al. 2015). Regarding canopy tree populations, our modeling results are consistent with this general view that late dry season fires are to be avoided as they are more detrimental to the potential for long-term persistence than are early dry season fires. Fire season alone is not the only factor, however—fire frequency also plays a role.

Regionally, outside of protected or aboriginal lands, eliminating late dry season fires entirely is likely impossible, mainly due to unauthorized and/or careless ignitions. With the very frequent and extensive fires occurring today near highways, some remote communities, and large cities such as Darwin (Russell-Smith et al. 2007, Elliott et al. 2009, Murphy et al. 2014), previously forested tracts of land will most likely become almost treeless, or indeed, grassy or shrubby savannas in the long run, due to loss of both fire-sensitive plants as well as the canopy eucalypt populations. In many locations in the Top End (including parts of KNP), the stage distributions of the eucalyptus canopy tree populations of today, compared to 30 yr ago, are consistent with a trajectory toward extirpation (P. A. Werner, *personal observation*).

Many managers have advocated the removal of sorghum from the landscape (Press 1987, Miles 2003). This is because the tall, annual grass is a major factor in the spread and destructive local effects of late dry season fires. Removal of sorghum could also prove advantageous to wildlife populations and built structures by reducing the areal extent and the direct and cascading effects of late dry season fires. However, as shown by our study, with respect to the lowland eucalyptus canopy populations, long-term persistence in the alternate, non-sorghum vegetation, can be severely compromised, especially if a late dry season occurs occasionally. Therefore, if the understory is switched to non-sorghum by wet season management burns (and assuming late dry season fires are eliminated), it would be very important to continue to provide early dry season fires every two to four years to reduce the competitive effects of non-sorghum understory on eucalypt sub-adult trees.

Assuming land managers have a strategic management goal of ensuring the long-term persistence of the canopy tree populations of the open forests, our study can inform shorter-term decisions about whether, and when, to ignite fires in a selected area. We do not attempt to proffer prescriptions for fire management but offer guidelines in the form of management actions that will positively affect a population of canopy trees, based on our model. Based on our key findings, eucalypt canopy trees must experience fire to persist (because total fire exclusion will eventually result in extirpation and replacement by fire-sensitive species), but not on an annual basis (because annual fires will lead to extirpation of the population as juvenile trees will be prevented from moving into the upper layers to replace larger trees that will ultimately die). Furthermore, the interannual timing of fires on a site should not be regular but incorporate variability with some longer fire return intervals (because stochastic interannual timing promotes the transition of smaller trees to larger sizes). For early dry season fires, unburnt patches are essential to provide opportunities for juvenile and sapling trees to transition to larger sizes and thus fires lit for management purposes should aim for patchy burns. Late dry season fires should be avoided if possible, or if not possible, not occur less than every five years (because these fires are particularly detrimental to tree growth and survival, especially of juvenile stages). Understory type should be identified and considered when planning the frequency of fires for a site (because

understory type affects both fire behavior and vital rates for small trees). These general guidelines are based on the results and insights from our model; should field data on the distribution of life-history stages of the target population be available at a particular site, then more specific recommendations could be made for short-term management actions that would enhance the long-term viability and stage distribution of the canopy trees.

In recent years, serious attempts have been made to incorporate Aboriginal traditional approaches to savanna fire management into contemporary management plans in the region. This includes a focus on the traditional patchy early dry season fires that help reduce the widespread occurrence of late dry season fires and has been advocated by several researchers and land managers (Russell-Smith et al. 2009, 2013 and references therein). In KNP, early, patchy dry season fires in 2016 and 2017 helped reduce what were previously extensive late dry season fires (Parks Australia 2016). Such a switch to more traditional fire management (early dry season, patchy, fires) will serve as a big step toward ensuring long-term persistence of the open forests.

The reintroduction of traditional fire regimes is to be applauded. However, simple reintroduction of traditional fire regimes may not yield an intended goal of sustaining the open forest canopy populations, at least over the next century or more. Special measures to ensure the timely replacement of the older, larger trees may be required because the previous decades of non-traditional practices undoubtedly decimated juvenile and sapling stages and/or made changes to understories. The resulting hysteresis effects due to low numbers of these life-history stages could be met by slight modifications (however temporary) during the recovery period from decades of non-traditional fire regimes.

Currently, strategic management plans are made mainly based on cultural considerations and predicted fire behavior per se. Whereas those considerations remain very important, we suggest that setting biological goals, coupled with an understanding of the biological and ecological responses to fires, would aid in strategic management planning.

Future research

Using our model and the transition and recruitment rates that we developed for 10 fire and understory scenarios, it would be possible to explore directly other fire intervals and/or combinations of seasonal fires and/or understory. There exists a myriad of possibilities for other simulations. Two other categories of potential future research that build on our model include Life Table Response Experiments (LTREs) to understand the relative importance of specific transition rates to population viability (Caswell 2000, 2001, 2014) and environmental extensions to explore, for example, carry-over effects of fire that may result in temporal autocorrelation in fire sequences. Both these types of future research are discussed in Appendix S8.

A further, particularly important area of research relative to the population dynamics of the canopy trees in humid savannas is the role of severe storms (cf. Appendix S8). Our study deals with disturbances (fire) that typically occur at very high frequencies, even annually. We did not include the effects of occasional severe storms, ranging from localized tornado winds to large cyclones that occur much less frequently here than in other coastal savannas (Williams and Douglas 1995, Cook and Goyens 2008). Nevertheless, such storms remove established canopy trees (Williams and Douglas 1995, Franklin et al. 2010) and could have significant effects on transient dynamics and long-term persistence, as has been shown for savannas on three other continents (e.g., references in Pascarella and Horvitz 1998, Platt et al. 2002, Gillson 2006). The probability that a canopy-removing storm will occur on any specific site in north-central Australia has not been calculated due to sparse human populations and settlements, but nevertheless, it most likely would be somewhere between one in 150–300 yr (Cook and Goyens 2008). This frequency is within the estimated life span of the oldest (largest) eucalypt trees (Werner 1986, Cook et al. 2005). The interactive effects of fire regimes, severe storms, and changing climate on canopy tree population persistence and the resulting savanna physiognomy is a potentially rich area for future research on any of the world's savannas.

Conclusion

Fire is a major driver of ecosystem dynamics in the humid savannas of northern Australia, as it is in other savannas of the world. We have demonstrated the utility of matrix populations models in integrating multiple data sets to form a general understanding of how the timing of fires and environment (e.g., understory type) influence the short- and long-term viability of canopy trees populations, and ultimately determine savanna structure (physiognomy). We found that fire is required and that fire-free intervals also are required for canopy tree persistence and that irregular fire intervals increase the probability of long-term persistence. Results can be attributed to the growth and survival of trees within various life-history stages, especially to juveniles and saplings. Fire regimes in many ecosystems across the world are being altered due to changes in land management and secondary effects of climate change. This study highlights the ecological complexity that must be understood to inform effective fire management.

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Data Availability

The computer source code (R code) to reproduce all our simulations is available online at https://github.com/sjpeacock/WernerPeacock2017.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2706/full

Appendix S1: Photos
Appendix S2: Study System: Canopy Trees: Biology and Ecology
Appendix S3: Discussion: Two Basic Assumptions of Model
Appendix S4: Sensitivities of Vital Rates
Appendix S5: Stochastic Simulations. Length, Autocorrelations
Appendix S6: Transient Dynamics: All Fire Scenarios
Appendix S7: Model Test: Predicting Population Dynamics in Kakadu National Park
Appendix S8: Discussion: Future Research